FIRM/S38 Rev 1

FAO Fisheries Synopsis No. 38 Rev. 1
(Distribution restricted)

FIRM/S38 Rev. 1
SAST - Knobbed wrack - 7,80(01)006,01

LIBRARY
MAY - 4 1971
FISH & WILDLIFE SERVICE

SYNOPSIS OF BIOLOGICAL DATA ON KNOBBED WRACK

Ascophyllum nodosum (Linnaeus) Le Jolis

Prepared by

E. Baardseth

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME, 1970

FAO
fish.
synop.
no. 38
rev. 1

DOCUMENTS OF THE FISHERY RESOURCES DIVISION OF FAO DEPARTMENT OF FISHERIES

Documents which are not official FAO publications are issued in several series. They are given a restricted distribution and this fact should be indicated if they are cited. Most of them are prepared as working papers for meetings, or are summaries of information for use of member governments, organizations, and specialists concerned.

DOCUMENTS DE LA DIVISION DES RESSOURCES HALIEUTIQUES DU DÉPARTEMENT DES PÊCHES DE LA FAO

Des documents qui ne figurent pas parmi les publications officielles de la FAO sont publiés dans diverses séries. Ils font seulement l'objet d'une distribution restreinte, aussi convient-il de le préciser lorsque ces documents sont cités. Il s'agit le plus souvent de documents de travail préparés pour des réunions, ou de résumés d'information à l'intention des gouvernements des pays membres, ainsi que des organisations et spécialistes intéressés. Ces séries sont les suivantes:

DOCUMENTOS DE LA DIRECCION DE RECURSOS PESQUEROS DEL DEPARTAMENTO DE PESCA DE LA FAO

Esta Subdirección publica varias series de documentos que no pueden considerarse como publicaciones oficiales de la FAO. Todos ellos tienen distribución limitada, circunstancia que debe indicarse en el caso de ser citados. La mayoría de los títulos que figuran en dichas series son documentos de trabajo preparados para reuniones o resúmenes de información destinados a los estados miembros, organizaciones y especialistas interesados.

FAO Fisheries Report **FIR /R (No.)**
FAO Fisheries Circular **FIR /C (No.)**
FAO Fisheries Synopsis **FIR /S (No.)**

Special groups of synopses are identified by symbols followed by classification numbers based on indexed code of "Current Bibliography":

SAST Data concerning certain species and fish stocks.

MAST Information on methods and subjects.

OT Oceanographic data.

IT Limnological data.

and

CART Information concerning fisheries and resources of certain countries and regions (FID/S).

Des catégories spéciales de synopses sont identifiées à l'aide de symboles suivis des chiffres de classification basés sur le code d'indexation de la « Current Bibliography »:

SAST Données sur certaines espèces et populations de poissons.

MAST Renseignements sur des méthodes et des sujets.

OT Données océanographiques.

IT Données limnologiques.

et

CART Renseignements sur les pêcheries et les ressources de certains pays et régions (FID/S).

Grupos especiales de sinopsis se distinguen con las siglas siguientes, seguidas por números de clasificación que se basan en las claves de los índices de la « Current Bibliography ».

SAST Datos relativos a ciertas especies y poblaciones.

MAST Sinopsis sobre métodos y materias.

OT Sinopsis sobre oceanografía.

IT Sinopsis sobre limnología.

y

CART Información sobre los recursos acuáticos vivos de algunos países y regiones (FID/S).

FAO Fisheries Technical Paper FIR /T (No.)

Special groups of Technical Papers are identified by:

RE Indexed lists of experts and institutions drawn from Registers maintained by the Fishery Resources Division.

CB Lists of periodicals, special sections of "Current Bibliography for Aquatic Sciences and Fisheries," special bibliographies and papers concerning documentation problems.

MFS Provisional editions of "FAO Manuals in Fisheries Science."

Des catégories spéciales de documents techniques sont identifiées à l'aide des symboles suivants:

RE Listes indexées d'experts et institutions tirées des registres tenus à jour par la Division des ressources halieutiques.

CB Listes de périodiques, des sections spéciales de la « Current Bibliography for Aquatic Sciences and Fisheries », des bibliographies particulières et des articles sur les problèmes de documentation.

MFS Editions provisoires des « Manuels FAO de science halieutique ».

Grupos especiales de documentos técnicos se identifican por las siglas siguientes:

RE Listas índices de expertos y de instituciones tomadas de los registros que se llevan en la Dirección de Recursos Pesqueros.

CB Listas de periódicos, secciones especiales de la « Current Bibliography for Aquatic Sciences and Fisheries », bibliografías especiales y trabajos relativos a los problemas de documentación.

MFS Ediciones provisionales de los « Manuales de la FAO de Ciencias Pesqueras ».

Some documents also have another identification, if, for example, they have been contributed to a meeting for which papers have been numbered according to another system.

Certains documents portent parfois d'autres numéros d'identification, par exemple, s'ils ont été préparés pour une réunion dont les documents ont été marqués à l'aide d'un autre système.

Algunos documentos tienen también otra identificación si, por ejemplo, son contribuciones a una reunión cuyos documentos han sido marcados con arreglo a otros sistemas.

SYNOPSIS OF BIOLOGICAL DATA ON KNOBBED WRACK

Ascophyllum nodosum (Linnaeus) Le Jolis

Prepared by

E. BAARDSETH

University of Bergen
Biological Station Espegrend
Blomsterdalen Norway

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, December 1970

Library
NOAA, National Marine Fisheries Service
SWFC Honolulu Laboratory F/SWC2
2570 Dole Street
Honolulu, HI 96822-2396

FAO
fish.
synop.
no.38
rev.1

PREPARATION OF THIS SYNOPSIS

A revision of the provisional version issued in August 1968, following the revised Outline for the Preparation of Synopses of Data on Species of Algae and their Utilization adopted in March 1970.

The preparation of the synopsis was promoted in view of the considerable importance of the species as a source or raw material for alginates. The provisional version was presented at the VI International Seaweed Symposium, Santiago de Compostela, 9-13 September 1968.

The author compiled the information available from the relevant literature and included also unpublished results obtained at the Norwegian Institute of Seaweed Research. Valuable unpublished data has also been communicated to him by scientists from various countries. Thus, the author wishes to acknowledge the information from Curator R.K.S. Lee (Canada), Dr. S. Lund (Denmark), Dr. J.T. Koster (Netherlands), Dr. A.D. Zinova (U.S.S.R.), Dr. R.T. Wilce (U.S.A.), Dr. C. MacFarlane (Canada), Dr. J. Seoane-Camba (Spain), Dr. O. Sundene and Mr. J.P. Taasen (Norway). He also wishes to thank his colleagues at the Norwegian Institute of Seaweed Research for the communication of unpublished results, and for correction of the manuscript.

The present version of this synopsis has been edited by the Marine Biology and Environmental Branch of the FAO Department of Fisheries.

Distribution :

FAO Department of Fisheries
FAO Regional Fisheries Officers
Regional Fisheries Councils and Commissions
Selector SM
Author

"Current Bibliography" entry :

Baardseth, E. (1970) 17-6M427
FAO Fish.Synops., (38):pag.var.
Synopsis of biological data on knobbed wrack Ascophyllum nodosum (Linnaeus) Le Jolis

ANW. ANE. Fucaceae - biological synopsis. Taxonomy and morphology. Geographical and ecological distribution. Metabolism - nutrition, growth. Life cycle - reproduction, phenology. Population - structure, density, mortality, biomass. Harvesting - techniques, seasons, yields. Protection and management. Utilization - food, fodder, manure, industrial products. Selected bibliography.

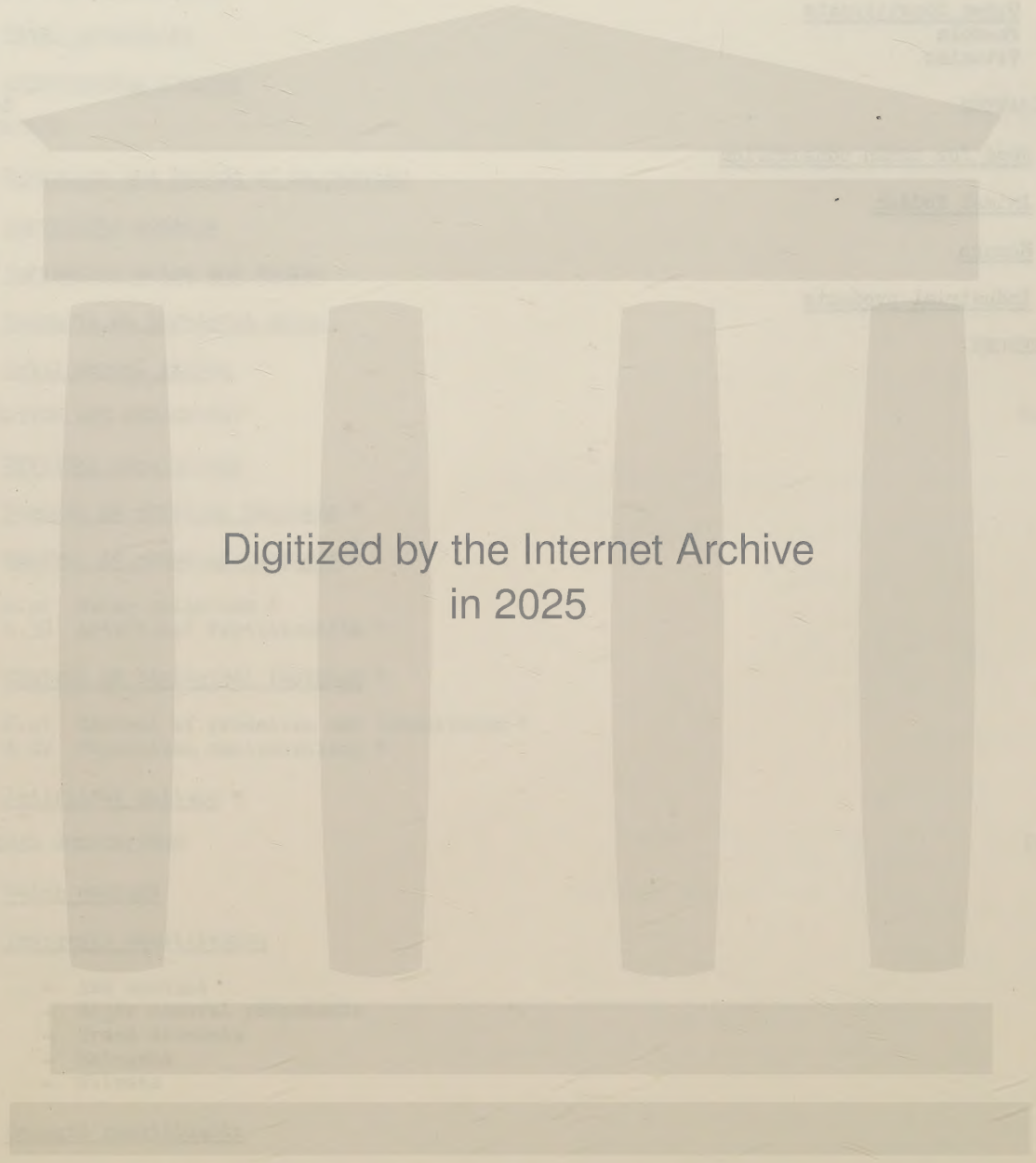
CONTENTS

		Page
1	IDENTITY	1:1
	1.1. Nomenclature	1
	1.11 Valid scientific name	1
	1.12 Nomenclatural synonyms	1
	1.13 Vernacular names	1
	1.2 Taxonomy	1
	1.21 Affinities, diagnosis	1
	1.22 Sub-species	1
	1.23 Genetic data	5
	1.3 Morphology and anatomy	5
	1.31 External morphology	5
	1.32 Anatomy and cytology	9
2	DISTRIBUTION, ECOLOGY AND METABOLISM	2:1
	2.1 Total area	1
	2.2 Local vertical and horizontal distribution	1
	2.3 Effects of ecological determinants	1
	2.4 Nutrition and growth	3
	2.41 Assimilation	4
	2.42 Respiration *	
	2.43 Nutrition *	
	2.44 Growth	4
3	LIFE HISTORY	3:1
	3.1 Life cycle	1
	3.11 Alternation of generations	1
	3.12 Nuclear phases *	
	3.2 Reproduction	1
	3.3 Phenology	1
	3.31 Seasonal variation in external appearance and morphology	1
	3.32 Seasonal variation in total fresh and dry weight	1
	3.33 Seasonal variation in other characteristics	1
4	POPULATION	4:1
	4.1 Structure	1
	4.11 Age composition	1
	4.12 Weight or size composition	2
	4.13 Sex composition	3

		Page
4.2	Density	3
4.21	Average density of defined areas	3
4.22	Variation in density with ecological and accidental factors	4
4.3	Mortality morbidity	5
4.4	Total quantities	5
4.5	Accompanying species	5
5	HARVESTING	5:1
5.1	Equipment and method of harvesting	1
5.2	Harvesting seasons	1
5.3	Harvesting areas and depths	1
5.4	Regrowth on harvested areas	1
5.5	Total annual yields	1
6	PROTECTION AND MANAGEMENT	6:1
6.1	Official regulations	1
6.2	Control of physical features *	
6.3	Control of chemical features *	
6.31	Water pollution *	
6.32	Artificial fertilization *	
6.4	Control of biological features *	
6.41	Control of predation and competition *	
6.42	Population manipulations *	
6.5	Artificial culture *	
7	CHEMICAL COMPOSITION	7:1
7.1	Water content	1
7.2	Inorganic constituents	2
	- Ash content	2
	- Major mineral components	2
	- Trace elements	3
	- Halogens	4
	- Nitrate	4
7.3	Organic constituents	4
7.31	Carbohydrates	4
	- Sulphated polysaccharides	5
	- Laminaran	6
	- Mannitol	6
	- Other Carbohydrates	6

		Page
7.32	Protein and amino acids	6
7.33	Fat	6
7.34	Pigments	6
7.35	Other Constituents	7
	- Phenols	7
	- Vitamins	7
8	UTILIZATION	8:1
8.1	Food for human consumption	1
8.2	Animal fodder	1
8.3	Manure	2
8.4	Industrial products	2
9	REFERENCES	

* As no information was available to the author these items have been omitted from the text



Digitized by the Internet Archive
in 2025

https://archive.org/details/fao-fisheries-synopsis_1970-12_38

1. IDENTITY

1.1 Nomenclature

1.11 Valid scientific name

The original name was Fucus nodosus L. 1753. The species was transferred to the genus Ascophyllum (as Ascophylla) by Stackhouse (Papenfuss, 1950), under the name A. laevigatum. The combination Ascophyllum nodosum was made by Le jolis in 1863.

1.12 Nomenclatural synonyms

A large number of synonyms has appeared (De Toni, 1895; Gib, 1957), of which the most important are:

Fucus nodosus L.
Ascophylla laevigata Stackh.
Ozothallia nodosa Decaisne et Thuret
Physocaulon nodosum Kütz
Halidrys nodosa Lyngb.
Fucodium nodosum J. Ag.
Halicoccus nodosus Aresch.

The free-living forms of Ascophyllum are known by another set of synonyms:

Fucus mackaii Turn.
Fucus scorpioides Hornem.
Ascophyllum mackaii (Turn.) Holm. et Batt.
Ascophyllum nodosum f. scorpioides. (Hornem.) Reinke.

1.13 Vernacular names

Being a plant of importance to coast dwellers, Ascophyllum is known by many popular names, the most important being:

Norway: Hesttang (horse-tang), grisetang (pig-tang). Also blaeretang, knopptang and boletang, these referring to its characteristic vesicles

British Isles: knobbed or knotted wrack, yellow tang, sea whistles, rockweed

Iceland: klóthang

Denmark: buletang

Sweden: knöltang

Canada: rockweed, goémon de roche, bottle kelp

France: goémon, varech (together with Fucus vesiculosus)

Netherlands: knotswier

Germany: knotentang

1.2 Taxonomy

1.21 Affinities, diagnosis

Ascophyllum nodosum (L.) Le Jol. belongs to the family Fucaceae of the order Fucales of the brown algae. It is usually considered to be the only species of the genus although an unattached form has been described as a separate species. Ascophyllum belongs to a well-defined group within the Fucaceae in which tufts of a special fertile shoots sprout from certain discrete points along the margin of the thallus. The group has a number of spectacular representatives in colder waters of the southern hemisphere, Ascophyllum being the only one from the northern. A near relative is the South African Axillaria constricta (Kütz.) Gruber (see for instance Fritsch, 1945).

A diagnostic description of the genus Ascophyllum, sufficient to distinguish it from other genera of Fucales, follows (see also Figs. 1 and 2).

Thallus linear, compressed, dilated at intervals by air vesicles, without a midrib. Primary branching dichotomous, initiated by the apical cell. Secondary branching bilateral, from initial cell located in marginal slits, producing either new vegetative shoots or tufts of special fertile shoots (receptacles). Slits distributed at more or less regular intervals all along both margins of the shoot, giving it a more or less serrated aspect, but never seen to grow into teeth or leafy expansions. Receptacles first linear, then spathulate and finally, at maturity, globular with a flat or triangular stalk. Oogonia with 4 eggs, very rarely with 8 (atavism?).

1.22 Sub-species

There can be no doubt that genetically different races of Ascophyllum exist, and in large numbers. Anyone who spends some time in an Ascophyllum field of some extension may easily discover differences between neighbouring plants which cannot be explained by external factors. Fig. 3, A-D, shows, for example, four different types of receptacles found on the same date and at the same locality (Leangen, Trondheimsfjord), but on different plants. One of them (A) was an abnormal, giant receptacle which itself produced normal sized receptacles. The others (B,C,D) are normal sized receptacles of three common types. In Galway, Ireland, the writer found a plant which had no lateral slits or shoots, but was otherwise normal in appearance.

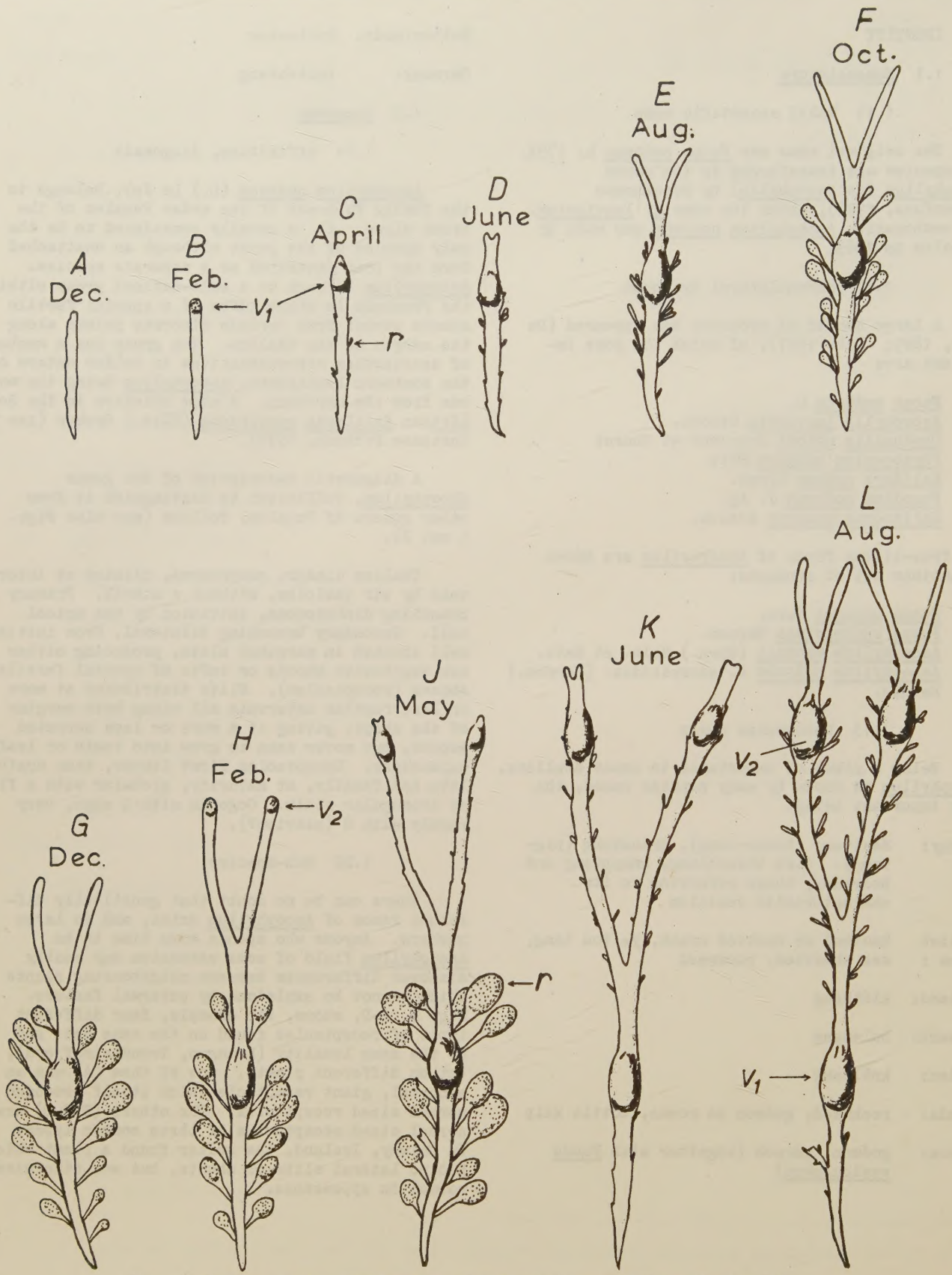


Fig. 1 Stages in the development of a lateral vegetative shoot, also showing the seasonal variation of the receptacles, v_1 and v_2 first and second set of contemporary vesicles. r = receptacles

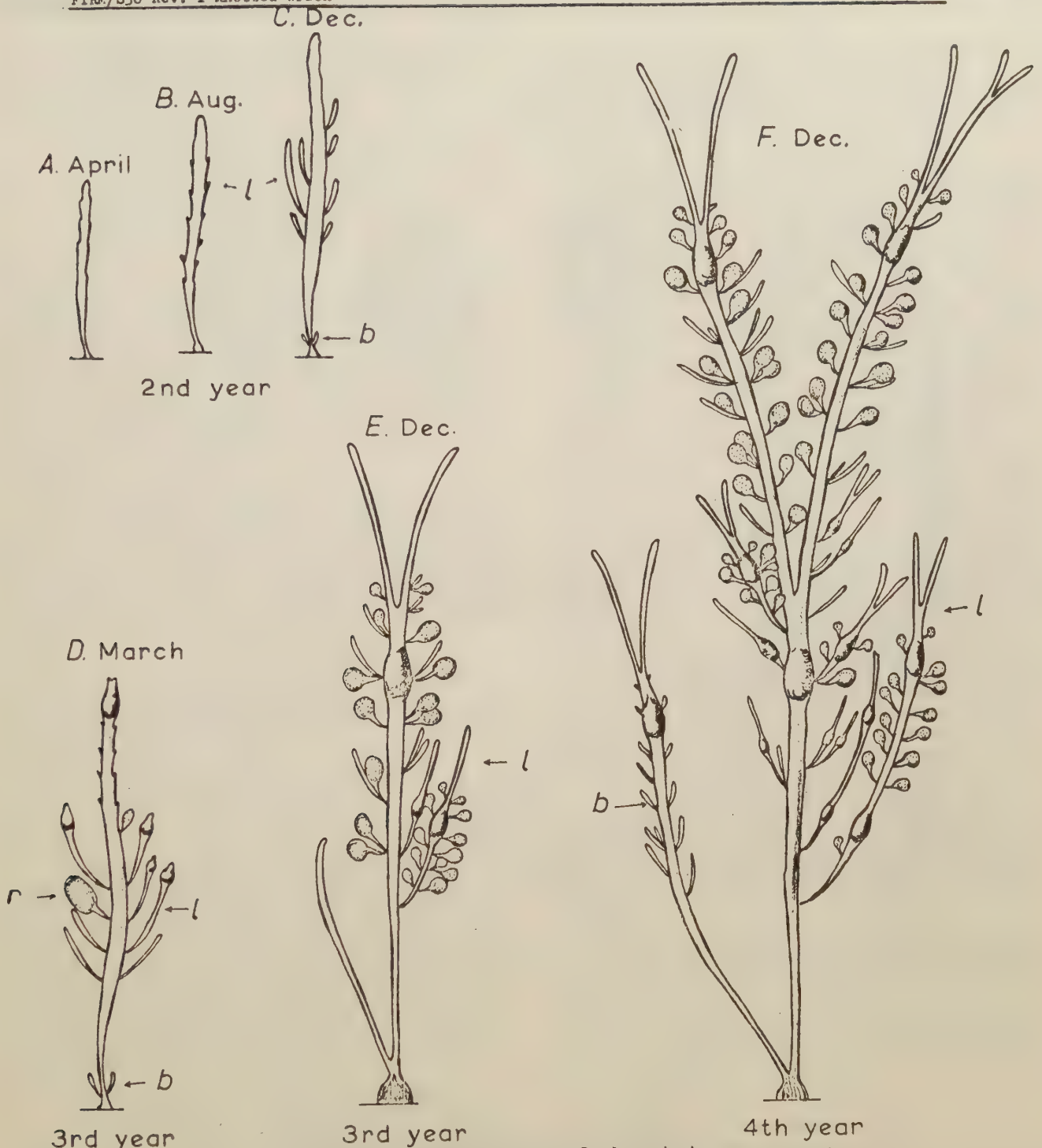


Fig. 2 Stages in the development of a base shoot
l = lateral vegetative shoots
b = new base shoots
r = receptacles

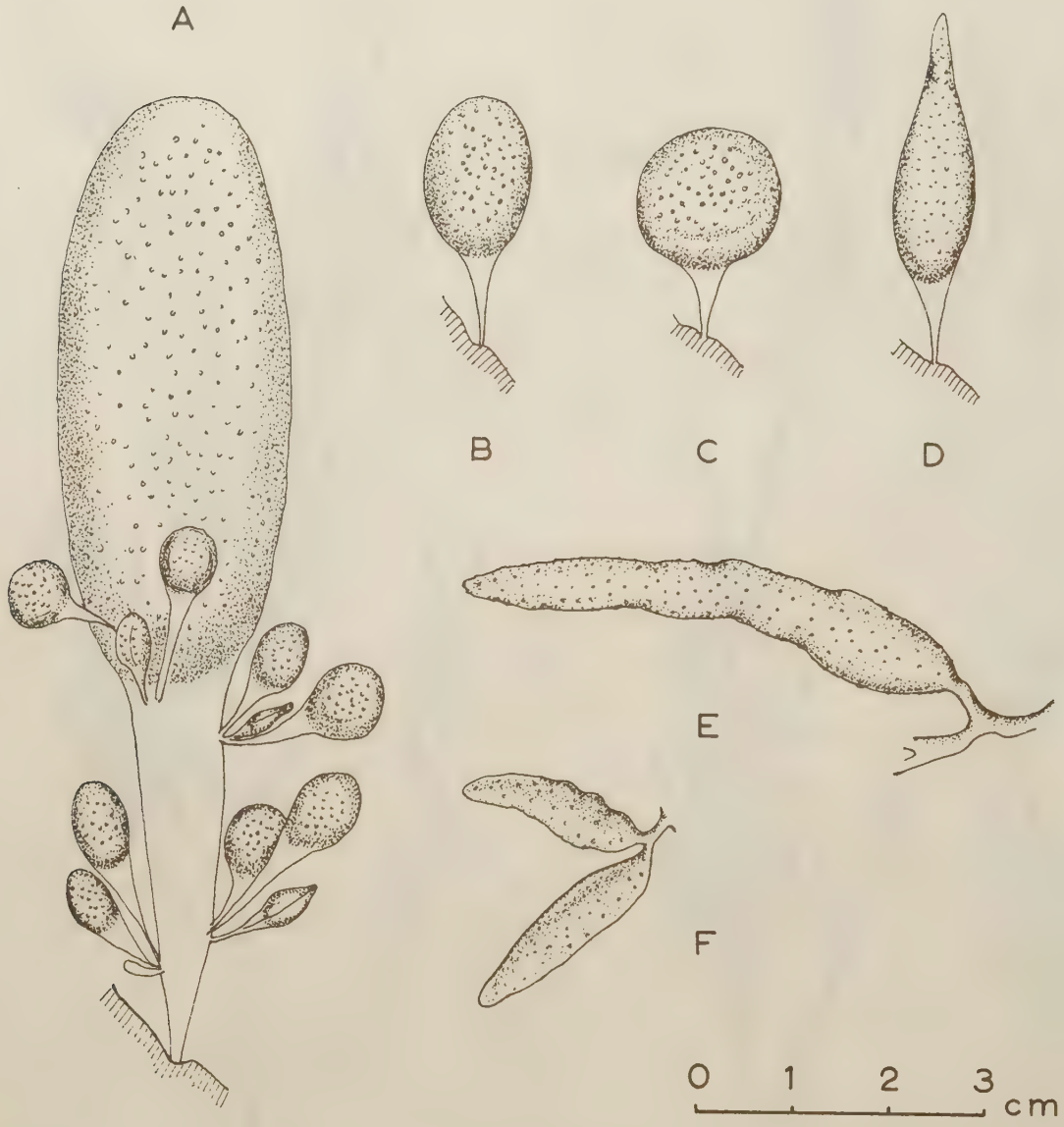


Fig. 3 Six types of receptacles: A – giant form with normal receptacles from lateral slits and from flat surface; B – oval; C – spherical; and D – acuminate receptacles. E and F – receptacles from A. mackaii (redrawn from Taylor and Harvey)

In addition to receptacle size and form, the following morphological features may undergo genetic variation:

1) the size and form of vesicles
2) the serration
3) the mean number of branches and the position of bifurcations relative to the vesicles

Fig. 4 shows four top portions of shoots from four neighbouring plants. The peculiarities shown in receptacles, vesicles, serration, and branching are all probably genetically determined because they are constant for all shoots of the same plant. There is thus ample justification for describing them as separate sub-species, each with a new name. The writer sees no reason to do so, however, because one would then see no end to the number of Ascophyllum sub-species.

Receptacle variation also exists in the unattached A. mackaii, to judge from the figures by Harvey (1871) and Taylor (1957) reproduced here as Fig. 3, E and F. In this case, it seems that, to a large extent, ordinary vegetative tips are transformed into receptacles, a condition which is extremely rare in attached plants.

1.23 Genetic data

According to an investigation by Lewis published in Godward (1966), the chromosome number of Ascophyllum is n = 32.

1.3 Morphology and anatomy

1.31 External morphology

Definition of the terms shoot and plant: A shoot of Ascophyllum is the complete morphological structure produced either by a fertilized egg or by a special initial cell, but without the interference of new initial cells. Thus, a mother-shoot may produce a number of initial cells which in turn may give rise to daughter-shoots. These daughter-shoots will be considered as separate units for statistical purposes and not as belonging to the mother-shoot. A shoot is thus essentially the same as a proliferation.

An attached plant of Ascophyllum may be defined as the assemblage of shoots and stumps of shoots arising directly or indirectly from a common holdfast. This definition is not always a precise one (Baardseth, 1955b) because the holdfast itself is a growing structure, which may produce several independent holdfasts. As a result, it may often be difficult to decide whether one single, irregularly outlined holdfast is present or whether there are many separate ones. A plant so defined thus becomes an inadequate statistical unit and is consequently better if the definition is based on the concept of a shoot when such characteristics as length, weight and age are considered.

Morphological description: The holdfast (Fig. 8) is a conical, compact disc with a rather irregular outline. Its colour is light yellow in peripheral actively growing regions, but is dark brown or even red or black in decaying parts. From the holdfast, shoots arise, which may be referred to as base shoots. When young, these are light yellow, but they darken with age. They are somewhat compressed (Fig. 2, F), dichotomously branched, with air-vesicles at intervals along the thallus, and they have no midrib. At more or less regular intervals along both margins are found small slits or cavities containing the initialling cells for development of new shoots (Fig. 5). Such shoots may be referred to as lateral shoots. They develop either into fertile shoots (called receptacles or fruit bodies, Figs. 1 and 2, r) or into vegetative shoots (Fig. 2, l). A slit may produce several shoots in one season and repeat shoot-production for several seasons, but its capacity for doing this decreases with age. Within a few millimetres below and above the colour-change demarcation line between holdfast and base shoots is a zone of great regenerative power. There are no slits in this region similar to those situated along the margins of the shoots, and the shoots arising from it are not bundled together like the lateral shoots. They represent new base shoots (Fig. 2, b) and their development is somewhat different from that of lateral shoots.

If a shoot, for some reason, loses all its apical growth points, it can no longer grow in length and will be referred to as a stump. These are quite normal living parts of an Ascophyllum plant. They may grow in thickness and produce new shoots, either laterally or basally.

There is also the possibility that a wounded surface may transform some of its cells into shoot initiators, especially when the wounds occur in young tissues.

The parts composing a plant of Ascophyllum may then be categorized as follows:

1 – Holdfast
2 – Stumps
3 – Base shoots (these are exclusively vegetative)
4 – Lateral fertile shoots (receptacles, fruit bodies)
5 – Lateral vegetative shoots
6 – Wound surface shoots (exclusively vegetative)

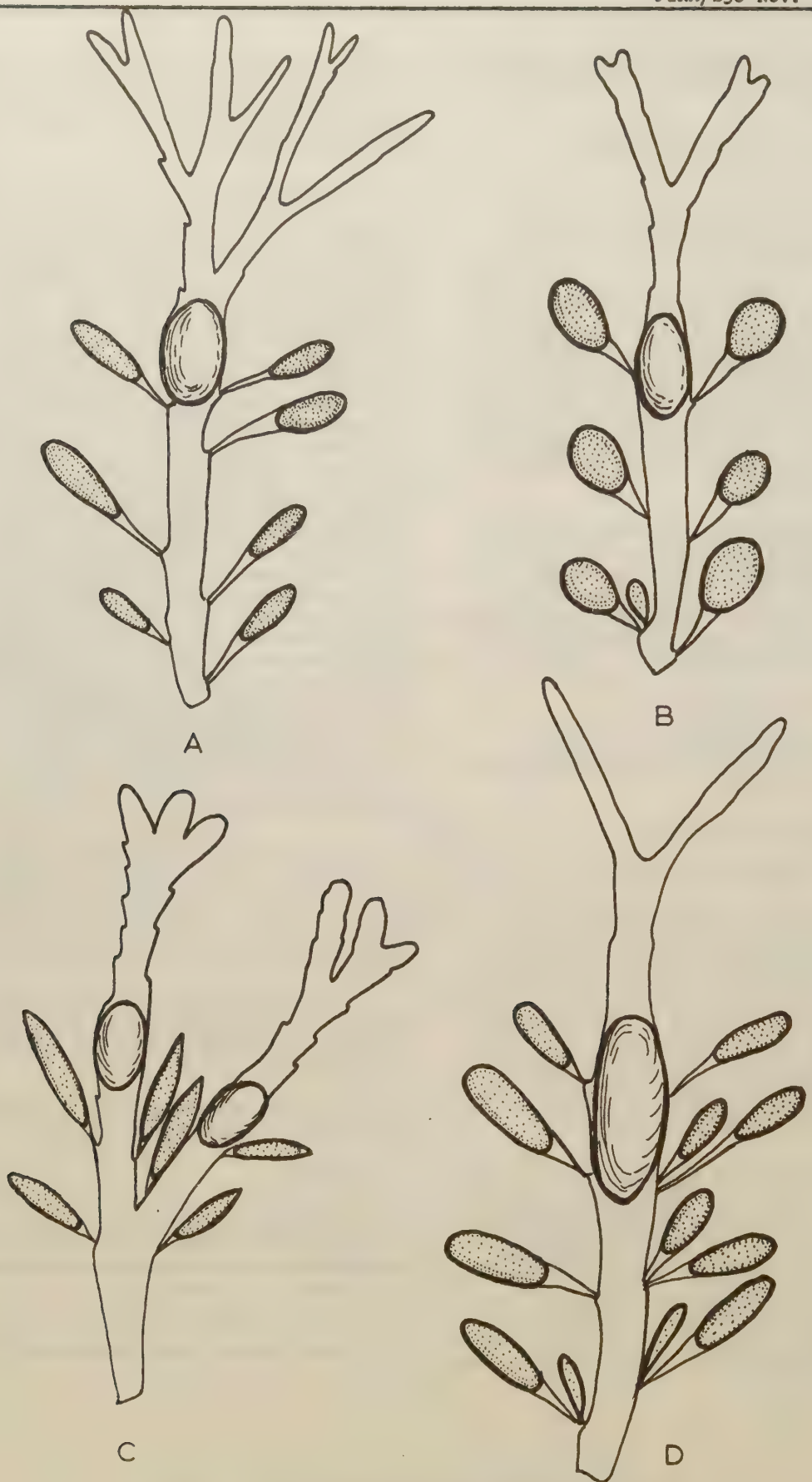


Fig. 4 Top portions from four different plants.
Leangen, Trondheimsfjord, Norway, Jan. 1969

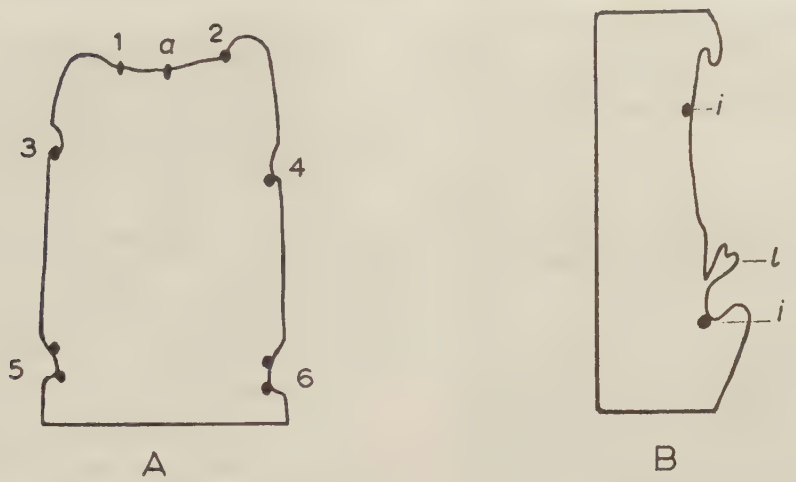


Fig. 5 A: Diagrammatic longitudinal section through an apex in plane of flattening

a = apical cell
1–6 = successive lateral initials sunk in marginal slits

B: Diagrammatic longitudinal section of a slit showing one outgrowing lateral (l) and two dormant initials (i). Redrawn from Fritsch (1945)

Phenological changes in morphology: The appearance of parts 3–6 varies according to age and season. In order to understand the seasonal changes in outward appearance and in the relative positions of the various kinds of shoots, it is advantageous to consider their complete life-history under the following three headings: a) receptacles, b) lateral vegetative shoots, and c) base shoots. The wound-surface shoots are virtually identical with the lateral vegetative shoots. The months given below for the various developmental stages apply to the Trondheimsfjord, Norway. The same stages may appear slightly earlier in southern localities, later in more northerly regions (Printz, 1959b). There is also considerable individual variation (Baardseth, 1970a).

a) Receptacles

1st year April–June:
The sprouting of receptacles usually begins in April, in the upper portion of the plant, from slits which have never produced shoots before (Fig. 1, C). It continues in May and June, in these months also from slits which have already produced a set of receptacles (compare Fig. 1, D and K). Slits may produce receptacles 6 times (Printz, 1926) or more, but progressively fewer each time.

June–August:
There is a general increase in length (Fig. 1, D and E) with formation of a cylindrical or spathulate structure, up to 1–2 cm of length.

September–October:
All shoots now begin to broaden at their tips, and at the same time cavities (conceptacles) appear in the cortex.

March–April:
The receptacles swell gradually due to the uptake of gas and water (Fig. 1, J).

April–May–June:
The receptacles ripen and the release of gamets from the conceptacles begins (Fig. 1, J). They are then shed in May and during a part of June.

Receptacles thus last for 12–14 months and undergo a definite seasonal development during this time. The time schedule may differ slightly from year to year, and is probably dependent upon external seasonal factors the nature of which is, however, unknown.

b) The lateral vegetative shoots

These arise from lateral slits, either in base shoots or in the stumps of base shoots, but in rare cases they arise also from slits in lateral shoots. Lateral shoots produced by a shoot which itself is lateral in position, practically always develop into receptacles.

1st year April–June:
The exact time of sprouting is difficult to establish because the first stages of growth are indistinguishable in appearance from those giving rise to receptacles.

When they are distinguishable (in August-September), the vegetative shoots have grown for some time, so that their sprouting probably takes place at about the same time as that of the receptacles.

July-December:
Nothing happens to the shoot except a general growth in length with production of slits, ending up with a flattened longitudinal structure like that in Fig. 1, A.

February-March:
At this time, some shoots produce a first vesicle at the tip (Fig. 1, B). There is a well defined period of vesicle-formation during the year (Baardseth, 1955b); David, 1943; Printz, 1926; Sundene, 1953) outside of which no new vesicles are formed. Not all shoots are liable to produce a vesicle even during the vesicle-formation period. It seems that a minimum weight, or possibly age, of the shoot is required for this ability (Baardseth, 1955b).

2nd year April:
The vesicle increases in size, the shoot continues to grow above the vesicle and the first set of laterals appear from the slits (Fig. 1, C).

May-August:
There is a general growth in length and thickness of the shoot, and frequent branching which is strictly dichotomous in its initial stages (Fig. 1, D and E). Later, the two daughter-branches may branch again but not always in the same manner. All branches of the same shoot usually reach the same length.

September-January:
Growth in length either stops or is retarded. Development of receptacles continues as described before (Fig. 1, F and G).

February-March:
Each tip of the shoot acquires a new vesicle (Fig. 1, H). This is the second set of contemporary vesicles, and the shoot is now almost 2 years old. The next year, at the same time, a third set of contemporary vesicles appears, and so on. The age of a lateral shoot may thus be determined by counting the number of sets of contemporary vesicles. A lateral shoot with n sets of contemporary vesicles (i.e. at the same level) is approximately n years old.

3rd year April:
A new set of laterals appears above the present set of receptacles (Fig. 1, J).

May-June:
The first crop of receptacles ripen and drop off (Fig. 1, J and K). From their slits new laterals sprout forth. These are a little delayed as compared to those mentioned above. They develop into the second crop of receptacles produced by this part of the shoot.

Further development takes place in the same manner, until the shoot for some reason loses its growing points. Although 20 year old shoots have been reported, they usually do not attain an age of more than 10-12 years.

c) The base shoots

These arise from the basal regenerative region of older base shoots, or from stumps of base shoots. After some time, they produce holdfast tissues of their own, so that sooner or later they appear to be attached directly to a holdfast and not to the mother shoot (Fig. 2, F, b).

Their seasonal development is similar to that of the lateral vegetative shoots, but the following differences must also be noted in addition to the different mode of attachment:

1. It probably takes about one year more before the first vesicle of the base shoots is formed (Baardseth, 1955b). Their age in years is consequently equal to the number of sets of vesicles plus one. There is, however, also a possibility that stunted or dwarfed shoots may take an even longer time before developing their first vesicles.

2. The first set of laterals of a base shoot is almost always vegetative, as distinguished from that of a lateral shoot, which is fertile, (compare Figs. 1, G and 2, C).

3. The second set of laterals is partly vegetative, partly fertile (Fig. 2, E). In later sets, the majority of laterals are fertile, but vegetative ones are also frequently seen.

It will be understood that Ascophyllum lends itself well to developmental and seasonal investigations, not only because the age of the whole shoot is determinable, but also because the age and life-history of every part of the shoot is known. As for the stumps, an exact age cannot be determined, but a minimum age can usually be assessed because they must be older than the lateral fixed to them.

Individual variation: The morphological description given above applies to well developed and fairly complete shoots like those in Fig. 1-2. However, a considerable amount of modification may occur, due to variation in external factors. First of all, there is variation from shoot to shoot within the same plant and from plant to plant at the same locality (Baardseth, 1955b and 1970a).

The weight distribution within narrowly defined groups of shoots has been studied for a regrowth population (Baardseth, 1955b). A characteristic feature was the extreme skewness in the distribution, which was found to increase with the passage of time. In a sample of stump shoots three years old, the lightest shoot weighed 130 mg and the heaviest shoot 17 000 mg. In a study of the quartiles of a time-series of samples, it was found that the shoots clustering around the upper quartile increased in absolute dry weight four to five times as fast as those around the lower quartile. Also, there is a strong positive weight correlation between the internodes along the axis. For Ascophyllum shoots, it is therefore tempting to enunciate a slogan; Once weak, always weak; once strong, always strong.

Individual variation in water and mineral content, is treated in sections 7.1 and 7.2.

Ecological variation: The appearance of Ascophyllum shoots and plants varies according to ecological conditions, but such variation has been little studied by exact methods. The use of the so-called "discriminant function" for such studies (see Bergquist, 1959) is well worth considering. There is no doubt, however, that ecological variation exists, on top of the individual variation. There is thus a general reduction in size and development; at high share levels, towards exposed localities, in rock-pools, in low salinity and highly polluted waters, etc.

The free-living forms (f. mackaii and f. scorpioides) are well known modifications due to habitats. Detached fragments of Ascophyllum are usually thrown ashore or are found floating on the surface. However, they occasionally get trapped in the littoral, for example when a peculiar configuration of the shore does not permit them to float out again with the tide. In the latter case, the fragments may develop into forms called scorpioides or mackaii which later multiply and branch independently of the original fragment. [For drawings see Taylor (1957) Pl. 27, Fig. 3 and Pl. 26, Fig. 2. Photo of mackaii vegetation see Lewis (1964) Pl. 32 A]. These forms are characterized by intense lateral and apical branching, by frequent suppression of vesicle and receptacle formation and by development of thin, almost cylindrical branches. They develop into isolated tufts or dense swards, often in considerable quantities on muddy or sandy bottoms. Gibb (1957) who has studied these forms extensively, recognizes a Baltic form, a beach form, a marsh form and a turf form.

From an industrial point of view, the free-living forms have the disadvantage of containing sand.

Ecological variation of chemical composition is referred in section 7.

1.32 Anatomy and cytology

The anatomy of Ascophyllum is fairly well known through the investigations of Oltmanns (1889) and others. The growth of an Ascophyllum shoot is governed by an apical cell (Fig. 5, A) which, in the period of active growth, cuts off cells laterally and basally. Two meristems are produced: 1) the surface layer of cells, called "meristoderm" by Sauvageau. This is present in all parts of the plant, but is not always active. It is responsible for the development and growth of the cortex of the plant (Fig. 6). Some cells of this meristem, situated along the median lateral line of the plant, are distinguishable as initiating cells (Fig. 5, A), which gradually sink in the well-known lateral slits. The initiating cells multiply and form the starting point of new shoots (Fig. 5, B). These at first grow by means of a three-sided apical cell which later becomes four-sided. 2) The subepidermal layers of cells in the apex divide at first both laterally and transversely to produce the medulla of the plant. Very quickly however, all lateral divisions stop. A few transverse divisions continue to occur, but after that the medullary cells do not divide any more. They grow in length and thickness, however, and develop in three ways, according to their final location into the medulla of a) receptacles (Fig. 6, B), b) fibres in vesicles, and c) the main vegetative thallus (Fig. 6, A). In the last case, a new type of cell, the hyphae, is being produced especially by the cell layers between cortex and medulla, and grows between the original medullary cells (Fig. 6, A). The hyphae and the medullary cells are easily distinguishable, for instance by their behaviour towards polarized light. Hyphae become progressively more numerous towards the base of the plant and the holdfast hardly consists of anything other than hyphae. They are absent in the inflated part of receptacles and in the fibres of the vesicle.

The intercellular spaces of the medulla are occupied by a water-insoluble substance (probably calcium and magnesium alginate and fucoidan) in the vegetative part of the thallus, by a complex soluble substance in the receptacle madulla and by gas between the fibres inside the air-vesicles. The intercellular substance of the receptacle medulla could, at certain times of the year (Baardseth, 1969), be squeezed out directly and analysed. It consisted of Na-, K-, Ca-, and Mg-alginate, fucoidan, inorganic salts (which increased from ca. 70% of the dry matter in March to ca. 94% in May when receptacles were ripe), and possibly of phenols and also gas bubbles. For presence of diatoms and fungal hyphae, see section 4.5.

The cytology of Ascophyllum has not been very extensively studied, at least not by modern methods. Ordinary light microscopy reveals the following major cell bodies:

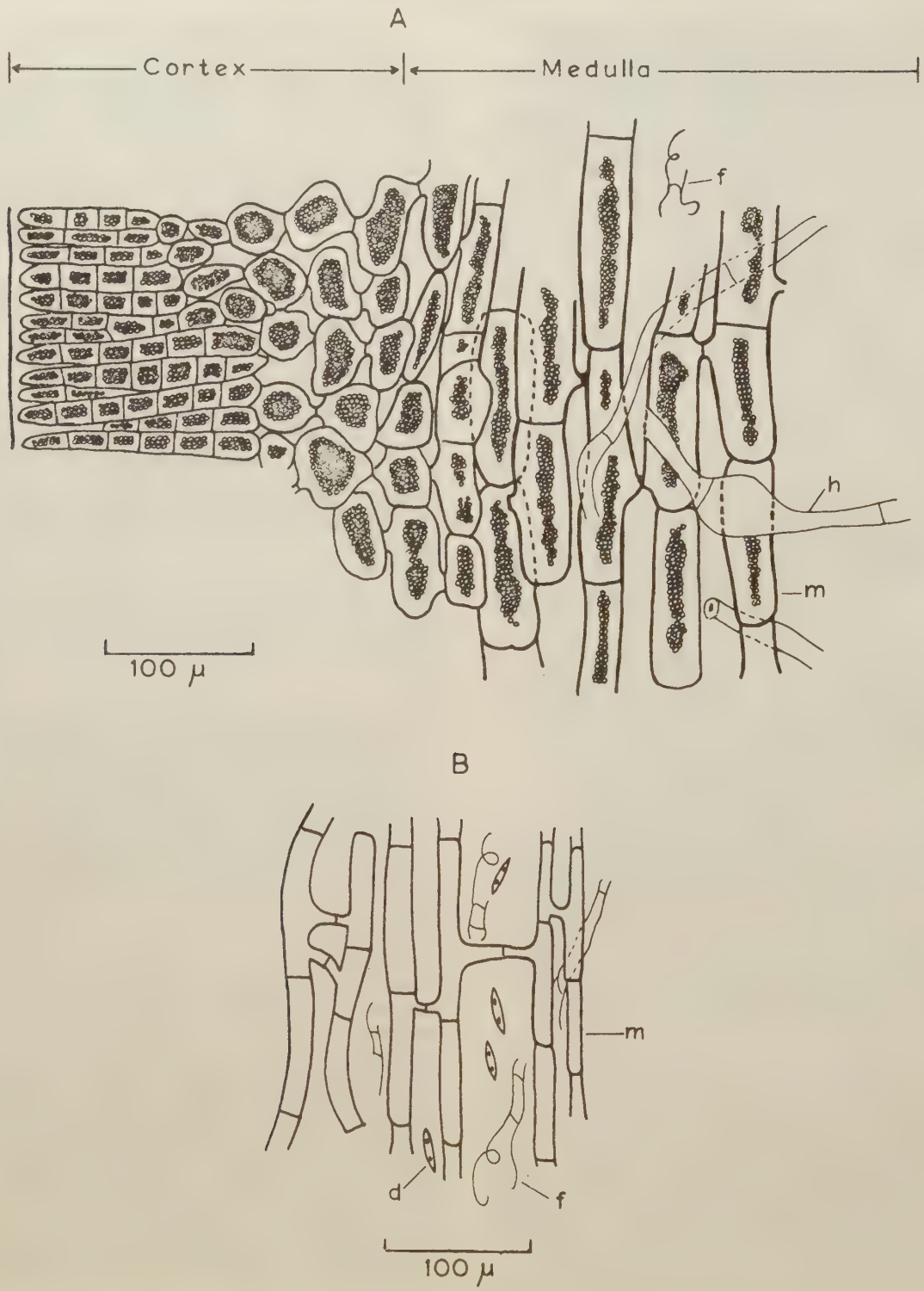


Fig. 6 A: Longitudinal section through cortex and adjoining part of medulla. Physodes indicated by dots.

B: Longitudinal section through receptacle medulla

m = medullary cell
h = hyphae
d = intercellular diatoms
f = fungal hyphae

a) Chromatophores which are distributed in cortical and also in medullary cells. The assimilatory capacity of the latter may be questioned, but nothing is known.

b) Nuclei, of which there is always one per cell.

c) Physodes. These occupy a large volume of the cell. They are numerous in cortical, medullary and hyphal cells in all parts of the plant, except in the medulla of the receptacles and in growing tips (Fig. 6, A). The physodes are best fixed with formalin and stained with bisdiazotised benzidine.

d) Fat vacuoles. Sudan-stainable vacuoles are seen, particularly in both extremities of medullary cells.

e) Wall. This consists of at least two layers but old medullary cells gradually become multi-layered.

f) Other cell bodies. Numerous small particles are frequently seen in the cells and in the intercellular substance. They have been little studied in Ascophyllum.

2. DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Total area

Ascophyllum is confined to the North-Atlantic coasts and the adjoining parts of the Arctic Sea (Fig. 7). Its exact geographic distribution is not completely known owing to gaps in the investigation of Arctic shores, but in the main the distribution of attached plants is as follows:

Northern limits: White Sea and island Kolgujev (A.D. Zinova, personal communication) but not further east (Kjellman, 1883; Zenkevitsh, 1963). Attached Ascophyllum has not been recorded for Novaya Zemlja or Spitsbergen, but is common along the Murman coast, and the coasts of Finmark (Norway) and Iceland. In Greenland, it extends up to 66°N (Jónsson, 1904) on the east side and to 77°N on the west side (R.T. Wilce, personal communication. See also Rosenvinge, 1926). It is furthermore recorded for Cumberland Sound on Baffin Island (Kjellman, 1883) and Ungava Bay, Labrador (Wilce, 1959).

Southern limits: Ascophyllum extends as far south as Viana do Castelo in Portugal, close to the Spanish border (Crisp and Fischer-Piette, 1959). It has been found cast ashore in the Azores several times, especially after storms, and it is accordingly assumed that it also occurs attached there (Schmidt, 1931). On the American coast, New Jersey appears to be the southern limit (Taylor, 1957).

Centre of distribution: Within these northern and southern boundaries, the largest quantities of industrially harvestable Ascophyllum are found in Western Norway, the British Isles, Northern France, Iceland and Eastern Canada.

Non-occurrences: Within the limits stated, attached Ascophyllum has been found in the Kattegat Sea as far south as Grenaa (S. Lund, personal communication) on the Danish coast, and Kullen on the Swedish coast (Levring, 1935), but it does not penetrate into the Baltic Sea. As the free-living form, f. scorpioides, Ascophyllum occurs, however, further south, for instance in the Danish belts, Kieler Föhrde, and Travemunde (Reinke, 1889). Attached Ascophyllum has not been recorded for the west coast of Denmark, Belgium or the French Basque coast between the bay of Gironde and the Spanish border (Crisp and Fischer-Piette, 1959; Feldmann and Lami, 1941). It is also absent in places where wave activity is too heavy and in polluted areas.

2.2 Local vertical and horizontal distribution

Vertical distribution: In regions with tides, Ascophyllum is an intertidal species, forming a zone at somewhat varying levels. Data of comprehensive measurements and analysis of these levels are missing in the ecological literature, but a general impression is that Ascophyllum occurs from slightly above midtide level down to somewhat above extreme low-water level. At one locality (Tarva, Norway, at ca. 64°N) with a maximum tidal range of 280 cm, the Ascophyllum zone was found between 50 and 175 cm above the extreme low water level. Judging from a diagram given by Lewis (1964), Ascophyllum seems to occupy similar levels in Scotland.

In regions without tides, it is permanently submerged, but usually occurs in shallow water. Here it occupies a zone with a lower limit of about 50–60 cm depth (Gislén, 1930). If the salinity of the surface layer is reduced, for instance near estuaries, the lower limit of the zone may be extended to a depth of about 330 cm.

There can be no doubt that the greatest quantities of Ascophyllum are found in regions with tides. It also seems to be a rule that the greater the tidal amplitude, the larger are these quantities. This is not due solely to an extension in width of the Ascophyllum zone, because it seems that the plant thrives better when it is exposed to the air during low tides. This is easily demonstrated when specimens in constantly submerged rock-pools are compared with those of the tide-exposed shore.

Horizontal distribution: Toward the edge of its geographical range, Ascophyllum occurs sporadically, but in the centre its distribution, can be said to be more or less continuous. There are, however, certain local limitations to its distribution, which will be considered in connection with certain ecological factors (see 2.3).

2.3 Effects of ecological determinants

The tolerance limits of Ascophyllum toward certain ecological factors may be determined, at least approximately from its regional and local distribution. Before drawing conclusions from such studies, the interaction between ecological factors and interspecific competition, must be taken into account.

(a) Sea temperature: It is hardly possible to indicate a minimum sea temperature below which Ascophyllum cannot live because of the simultaneous influence of ice. It thrives, however, in a perfect condition, in Finmark at winter and summer temperatures of about 3°C and 7°C, respectively, in Northern Iceland (1–10°C), and in Labrador (-1.78° and 4°C). The southern boundaries of Ascophyllum appear to be largely determined by a maximum summer temperature above which it cannot live. This is about 22°C (Setchell, 1920, 1922) on the American coast. At the southern limit in Portugal there is a summer sea temperature of about 19°C, while at the Azores it is about 23°C (Schmidt, 1931).

Fig. 7 Geographical distribution of Ascophyllum

At shores with large quantities of Ascophyllum, summer sea temperatures between 10 and 16°C are frequently recorded, but it would be difficult to determine an exact optimum temperature from its distribution.

(b) Ice: It is most probably ice which prevents Ascophyllum from penetrating further north into the Arctic regions (Kjellman, 1883). In western Spitsbergen (Svendsen, 1959) for instance, where the sea is usually frozen from December until May, Ascophyllum is absent, although other, more fast-growing littoral algae are present. However, the alga can apparently tolerate a certain amount of ice, because the White Sea and the Davis Strait are frozen during winter. Wilce (1959) writes that attached Ascophyllum under such conditions is more frequently sublittoral than littoral. Also, in regions with no permanent winter ice, Ascophyllum may, during periods of severe cold, be embedded in a mantle of ice for several days without apparent injury Printz (1957) reports, however, almost complete disappearance of Ascophyllum during the severe winters of 1939-42 and 1946-47 in Southern Norway when this part of the coast was blocked with ice. It is probably the movement of the ice rather than the actual freezing which is destructive to Ascophyllum.

(c) Salinity: Ascophyllum thrives in sea-water of normal salinity, but may also tolerate a certain amount of dilution or diurnal salinity changes near river outlets. The distribution of Ascophyllum in localities with a salinity gradient has been studied (Alstadsaeter, 1954; Doty and Newhouse, 1954; Fischer-Piette and Seoane-Camba, 1962, 1963; Gislén, 1930; Jorde and Klavestad, 1963; Larsen and Haug, 1958). Salinities at such places vary considerably according to tides and rainfall which makes it difficult to determine precise lower tolerance limits from such studies. Doty and Newhouse report Ascophyllum from estuarine waters with a maximum salinity of 17.3 o/oo and a minimum of 0.0 o/oo.

In the inner part of Hardangerfjord, Norway, Ascophyllum still exists at salinities of between 10 and 15 o/oo in May-August (Alstadsaeter, 1954; Jorde and Klavestad, 1963).

(d) Exposure to waves: It is well known that Ascophyllum cannot resist very heavy wave action. In passing from protected places to the open sea, it can be observed that the number of plants become progressively reduced, and that they consist increasingly of stumps and short-lived shoots. The plants sometimes find a foothold on shores facing the open sea, but in such cases their development is always extremely reduced and it occurs only in places with at least some local protection.

Although the wave-exposure factor is important in determining the local distribution of littoral organisms, direct measurements are not practicable. A measure correlated to this factor, viz. the sector of open sea facing a locality (Baardseth, 1970b), has been taken instead. This measure was called the exposure index and was employed in classifying the types of sampling areal units into protected, semi-exposed and fully exposed. By sampling the Norwegian West coast between the latitudes 60° and 67°N on the basis of a sampling unit of 463 463 m, it was found that 93.7% of the protected units, 73.4% of the semi-exposed units and 28.6% of the fully exposed units contained Ascophyllum. This series of percentages thus expresses the correlation between exposure and occurence of the species in a quantitative way, but this correlation could evidently be assessed more precisely by decreasing the size of the sampling unit and by excluding all units with an unfavourable sub-stratum.

(e) Sub-stratum: Ascophyllum requires rocks or stable stones for attachment. In fact, its competitor Fucus vesiculosus appears to be able to occupy a stony beach more easily than Ascophyllum.

(f) Pollution: Ascophyllum was a common alga in the inner part of the Oslofjord some 50 years ago, but has almost disappeared now, probably due to the increased sewage pollution (Grenager, 1937).

In laboratory experiments Boney (1968) has tested the influence on different algae of the main detergents which were used for emulsifying the oil spilled during the Torrey Canyon disaster. He describes their effect on Ascophyllum receptacles and conseptacle contents as well as that on Ascophyllum spermatozoids.

(g) Other ecological factors: Light, inclination, competition, epi-endophytes, and human influence may of course all affect the local or regional distribution of Ascophyllum, and also its density, but the importance of these factors is not so obvious as of those stated above.

The geographical and local distribution of Ascophyllum thus shows that the species is eurythermal, with a wide temperature tolerance (from 0°C to about 20°C); euryhaline with a salinity tolerance of about 15 to 37 o/oo, that it occurs in protected localities, requires firm sub-stratum and is somewhat sensitive to pollution.

2.4 Nutrition and growth

Physiological processes in Ascophyllum such as assimilation, respiration, growth, etc. have been little studied by experimental methods.

2.41 Assimilation

The assimilation surplus, determined by the O_2-method of Winkler, has been studied for various depths and months (Levring, 1947; Printz, 1950) and for parts of the plant at different ages (Printz, 1959a). Nath (1967) studied the uptake of O_2.

2.44 Growth

The increase in mean weight of internodes (Printz, 1926) and in mean weight of shoots (Baardseth, 1955b) with time has been determined. David (1943) studied the length increase for various parts of the shoot. The effect of auxins on the growth of Ascophyllum was reported by Davidson (1950).

3. LIFE HISTORY

3.1 Life cycle

3.11 Alternation of generations

Like all other species of Fucales, Ascophyllum has only a sexual generation. It is furthermore impossible to assign a fixed life cycle to the species, in the sense of a plant's germination, growth to maturity, reproduction, ageing and death, because a plant is constantly being renewed from the the base. When speaking of a single shoot, however, the life span is limited. Its development is described in section 1.31 and its age and weight, in 4.1.

3.2 Reproduction

Ascophyllum reproduces vegetatively by basal shoots which gradually become detached from the mother shoot (see Fig. 2) or by lateral shoots from loose fragments (f. scorpioides or f. mackaii).

Sexual reproduction is oogamous with eggs and sperms produced in the conceptacle cavities within the receptacles (cf. 1.31). Extrusion of eggs and sperms from the conceptacles is easily accomplished by exposing ripe receptacles to air over-night. Fertilization is also readily obtained by mixing eggs and sperms in sea water. The settling of zygotes and the production of a rhizoid take place within the first ten days after fertilization (Sundene, MS), but after that, growth seems to be extremely slow. Sundene managed to keep germlings alive for 5 years, partly in culture and partly in the sea. The germlings reached a size of not more than 0.1-0.2 cm after one year of growth and 1.0-1.5 cm after two years. The growth rate of germlings is thus extremely slow in comparison to that of its competitor, Fucus vesiculosus, and the chances of their being covered by diatoms or attacked by Littorina are greater. This may explain the scarcity of Ascophyllum germlings in nature, a fact which was commented upon by Oltamanns as early as 1889.

Two year old plantlets had new base shoots in Sundene's experiment, and the first air-vesicle and receptacle appeared after the plantlets had grown for five years.

Reproduction by fertilized eggs is thus inefficient in the case of Ascophyllum, but must necessarily be successful from time to time, as otherwise settlement on isolated stones would be impossible. However, vegetative reproduction by base shoots is by far more important.

Sundene also reported bud-like structures on the rhizoids of germlings, but pointed out that they have to be studied more closely.

3.3 Phenology

3.31 Seasonal variation in external appearance and morphology (see section 1.31)

3.32 Seasonal variation in total fresh and dry weight

The fresh weight of Ascophyllum varies throughout the year. The changes in fresh and dry weights of three sets of Ascophyllum plants were followed from month to month in two contrasting habitats (Baardseth, 1970a). The main results (Table I) of this investigation were as follows:

(a) Summer (June-August): The plants increased their absolute dry weight from a low value in June to a high value in September-October. This is due to growth of vegetative parts and simultaneous building up of a new crop of receptacles. In addition, destructive forces may not be as active during the summer as they are during the rest of the year.

(b) Winter (September-March): No significant increase in dry weight took place during this period. The weight either persisted at a constant level, or dropped as a result of the action of destructive forces.

(c) Fruiting season (April-May): The fresh weight increased considerably due to the uptake of water by the ripening receptacles. The dry weight sometimes showed a temporary increase, probably due to the uptake of salt. After the shedding of receptacles, a loss in dry weight was usually apparent, although a simultaneous growth of vegetative parts counteracted this to a certain extent.

The densities at the two localities investigated were therefore usually at a maximum in late summer and at a minimum in June, immediately after shedding of the receptacles. However, it must be noted that accidents may sometimes disturb this simple picture.

3.33 Seasonal variation in other characteristics

For seasonal variation in water, inorganic and organic contents see sections 7.1, 7.2 and 7.3, respectively. Seasonal features, of the endophytic diatom population, are treated in section 4.5.

TABLE I

Seasonal variation in fresh, live weight and in estimated dry weight of three sets of Ascophyllum plants

Set 1 Leangen 1956–58			Set 2 Leangen 1963–65			Set 3 Byneset 1963–65		
Date	Fresh weight (kg)	Dry weight (kg)	Date	Fresh weight (kg)	Dry weight (kg)	Date	Fresh weight (kg)	Dry weight (kg)
5/ 8/56	112.9		5/11/63	125.6	30.5	6/11/63	108.1	30.0
3/ 9/56	136.8		28/11/63	123.8	29.5	4/12/63	105.4	28.8
2/10/56	165.4	40.1	13/ 1/64	130.1	28.9	15/ 1/64	83.0	21.0
1/11/56	182.4	41.7	19/ 2/64	117.9	27.9	18/ 2/64	86.9	22.6
30/11/56	157.5	38.8	18/ 3/64	128.3	28.5	19/ 3/64	69.2	19.6
14/ 1/57	145.4	38.3	15/ 4/64	176.2	31.6	16/ 4/64	72.8	18.1
12/ 2/57	155.2	33.3	28/ 5/64	110.2	27.8	29/ 5/64	71.1	16.7
12/ 3/57	182.6	37.2	27/ 6/64	122.7	31.9	29/ 6/64	73.3	20.6
11/ 4/57	161.0	31.5	5/ 8/64	124.0	34.2	4/ 8/64	85.1	25.4
10/ 5/57	150.1	28.6	4/ 9/64	152.0	37.0	5/ 9/64	110.2	30.2
8/ 6/57	94.8	25.3	24/10/64	157.7	37.5	26/10/64	103.9	29.2
12/ 7/57	117.1	32.0	16/12/64	155.4	34.4	17/12/64	108.2	28.3
22/ 8/57	155.1	41.3	19/ 2/65	169.4	35.3	20/ 2/65	114.6	28.0
5/10/57	188.4	44.9	2/ 4/65	170.6	28.7	3/ 4/65	117.4	24.2
9/11/57	184.5	44.5	27/ 4/65	188.5	34.0	28/ 4/65	124.0	29.1
5/12/57	181.2	41.0	4/ 6/65	153.5	37.8	5/ 6/65	127.2	29.5
17/ 1/58	174.3	39.0						
14/ 2/58	168.3	37.6						
14/ 3/58	157.7	37.1						
15/ 4/58	224.2	43.7						
23/ 5/58	236.8	37.2						
24/ 6/58	92.9	26.7						
28/ 7/58	116.1	32.2						
12/ 9/58	150.7	38.3						
11/10/58	118.7	33.1						
8/11/58	130.2	34.0						
9/12/58	109.3	28.2						

4. POPULATION

4.1 Structure

4.11 Age composition

The age of an Ascophyllum "plant" cannot be determined. Because of its vegetative reproduction, a "plant" of Ascophyllum as it is seen today, might have originated from a fertilized egg thousands of years ago. Therefore, the age of an Ascophyllum "plant" is a meaningless variable, but if shoots are considered, their age can be determined. Two examples are given in Table II.

In two random samples of Ascophyllum shoots, one from Leangen, Trondheimsfjord 1959, and the other from Galway, Ireland 1948 (Baardseth, 1955b) the numbers of base and lateral shoots in each year-class were counted. In the Galway sample, only stump shoots were counted, the laterals on base shoots being disregarded, whereas in the Leangen sample, all lateral shoots were included. In both samples (Table II), there appeared to be a steady decline in number of shoots from one year-class to the next (the few exceptions to this rule may be due to sampling fluctuations). This age distribution indicates that the "birth rate" within an Ascophyllum shoot population is fairly constant from year to year. There is at least no year-class with a conspicuously abnormal number, such as may be found within animal populations. The "death-rate" is also of the usual type, with a very heavy mortality at the beginning of life, then a decrease until a minimum mortality amongst the middle-aged shoots is reached, and finally a gradual increase with increasing age. The entire maximal life-span appears to be 11-13 years in these two localities. In localities with greater wave exposure, the maximum age will be less.

Harvesting will probably alter the "birth-" and "death-rate", but very little detailed information is available about this.

TABLE II

Number of shoots in each year-class in two samples of Ascophyllum

Year class	Leangen, Trondheimsfjord 1959		Galway, Ireland 1948	
	Number of base shoots	Number of lateral shoots	Number of base shoots	Number of stump shoots
0	*)	*)	5224	4712
1	*)	1267		
2	35	727	1009	3177
3	46	491	727	1553
4	61	328	472	1070
5	34	168	446	808
6	43	64	398	637
7	27	43	218	360
8	18	5	103	31
9	13	-	29	22
10	2	-	26	18
11	1	-	12	4
12	-	-	8	5
13	-	-	1	1

*) Not counted

4.12 Weight or size composition

The distribution of the values of dry weight of shoots within the several year-classes has been studied for harvested areas (Baardseth, 1955b). The regrowth on such areas produces new shoots that are heavier, on an average, than corresponding shoots from uncut areas. Table II gives the total and mean dry weight of the several shoot categories within a sample from Leangen, Trondheimsfjord (28 October 1959). The zero year-class is not included.

It will be seen from Table III that the weight-proportion between the stumps and the stump shoots is 2.7 : 3.3, whereas that between base shoots and their lateral vegetative shoots is 5.2 : 1.9. Stumps are thus able to carry a heavier load of lateral shoots than are actively growing base shoots. This fact may have several explanations. One of them may be that a fracture or cut increases the stimulus of shoot sprouting and growth (compare for instance Fig. 8, A and B).

The estimate of the mean weight of shoots involves a large sampling error, but it seems safe to conclude that in this sample, the means are about equal for the three categories of shoots in the first 4 year-classes, but after that, there is an increasing tendency for base shoots to take the lead, with stump shoots second, and laterals on base shoots last.

TABLE III

Total dry weight and mean dry weight of the shoots in each year-class and each of the three categories base shoots, stump shoots, and lateral shoots on base shoots. Sample from Leangen, Trondheimfjord, 28 October 1959

Age in years	Total weight in g			Mean dry weight in g		
	Base shoots	Stump shoots	Lateral shoots on base shoots	Base shoots	Stump shoots	Lateral shoots on base shoots
1		133.2	81.8		0.17	0.16
2	20.9	183.8	209.9	0.6	0.58	0.51
3	58.5	350.3	459.2	1.3	1.6	1.7
4	181.0	360.4	626.3	3.0	2.5	3.4
5	264.5	830.0	193.4	7.8	7.0	3.9
6	883.1	693.9	49.4	20.5	14.5	3.1
7	1513.3	619.3	108.6	56.1	19.3	9.9
8	800.2	160.7	173.3	44.4		
9	787.3			43.7		
10	628.9					
11	72.0					
Total weight	5209.7	3331.6	1901.9			
Weight of stumps		2721.5				

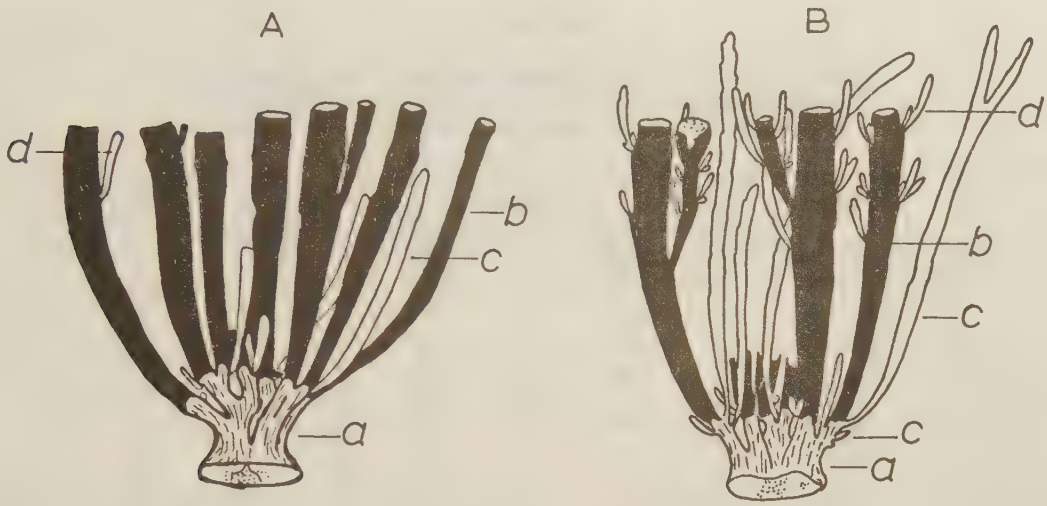


Fig. 8 A: Remnant parts of a plant just after cutting

B: Same, ca. 5 months after the cutting

a = holdfast
b = stump
c = base shoot
d = stump shoot

4.13 Sex composition

The Ascophyllum population consists of male and female plants. There is no sporophyte generation. In one sample of 47 plants (Trolla, Trondheimsfjord) there were 29 females and 18 males, in another (Leangen, Trondheimsfjord) of 56 plants, there were 30 females and 26 males.

4.2 Density

4.21 Average density of defined areas

The density of seaweed populations are best measured as fresh weight per unit area. This measure is also of practical interest.

The density of an Ascophyllum zone has been extensively studied (Baardseth, 1955a, 1958b; Baardseth and Grenager, 1961; Chapman, 1950; Gislén, 1930; Walker, 1947), especially in connection with the total standing crop over large stretches of coast.

The former practice of selecting squares subjectively for cutting and weighing gave an unreliable, false impression of the density. In order to get objective density figures for practical use, it was necessary to ensure (Baardseth, 1955a) that: a) The Ascophyllum zone be well defined and delimited. b) The sampling within this zone either be strictly random or follow a scheme equivalent to random sampling.

To study the density distribution within an apparently homogeneous and luxuriant Ascophyllum zone (Hestvaer, Norway at 64°N), the zone was divided by equidistant transects running perpendicular to the shore-line, and all the way from the upper to the lower boundary of the zone. In all, 623 quadrates of $\frac{1}{2}$ m^2 in size were cut and weighed within this particular zone. The data from each quadrate are given in Table IV, where they are arranged in weight groups and also according to the position of the quadrates in the upper or lower half of the zone (20 quadrates were excluded because they belonged to both). This Ascophyllum population was growing on a rocky, gently sloping but somewhat uneven shore and the vegetation was, as can be seen from the table, characterized by:

(a) A number of zero values (60 out of 623), i.e. quadrates devoid of Ascophyllum. In order to get a correct mean density, these zero values were included in the calculation. When squares are selected subjectively for density studies, zero values tend to escape notice or to be ignored. Only random sampling reveals their correct number.

It will be seen that there is a greater frequency of zero values in the lower half of the zone than in the upper one. This is a frequent characteristic of an Ascophyllum zone, giving it a "patchy" appearance in the lower part and a more homogeneous one in the upper.

TABLE IV

Frequency distribution of fresh weights of Ascophyllum in ½ m² quadrates. Hestvaer, Frooyene, Norway, August 1954. Rearranged from Baardseth, 1955a

Weight kg per ½ m²	Number of quadrates		
	Upper half	Lower half	Whole zone
0	19	41	60
0.1–1.9	114	81	200
2–3.9	92	71	168
4–5.9	44	40	87
6–7.9	21	30	55
8–9.9	6	14	22
10–11.9	3	9	12
12–13.9	1	7	8
14–15.9	1	2	4
16–17.9		2	2
18–19.9		2	2
20–21.9		1	1
22–23.9		–	–
24–25.9		1	1
26–		1	1
Total	301	302	623
Means kg/½ m²	2.8 ± 0.14	3.9 ± 0.24	3.4 ± 0.14

(b) The distribution of density values is very skew, which requires a large number of observations in order to get the same accuracy as in the case of a normal distribution.

(c) The percentage of very high density values is greater in the lower than in the upper part of the zone. Also, the mean is significantly higher in the lower zone in spite of the greater number of zero values.

The mean density obtained during the investigations described above 6.8 kg/m² ± 0.28, is valid for the Ascophyllum zone of this particular shore which was 250 m long and in average 12.9 m broad. To obtain a density value for large areas, a method of sampling along equidistant parallel lines was tried (Baardseth and Grenager, 1961). The result for one district, Hitra – Frøya (876 km²), was 4.33 (± 0.369) kg Ascophyllum per m² where the area considered covered the range between the upper and lower-most Ascophyllum specimens.

4.22 Variation in density with ecological and accidental factors

In another large-scale investigation of insular and fjord districts (Grenager and Baardseth, 1966, and Baardseth, 1970b), the sampling was done following a two-stage system involving an initial division of the district into large primary units (463 × 463 m), a number of which were then randomly selected and sub-sampled. Each of the sub-samples covered an area of 1 m² (secondary unit). By this method of sampling, it was possible to distinguish between density variations: 1) within a primary unit (referred to as accidental variation), 2) between primary units (local variation) and 3) between districts (regional variation).

Within the rocky portion of the area between the upper and lower border of the Ascophyllum zone, the Ascophyllum density varied between zero and 26 kg/m² in a certain district of the Norwegian west coast (64°–65°N) with a general mean of 5.2 kg/m². A local variation was shown to be present on top of the accidental one.

TABLE V

Overall densities of Ascophyllum, in kg fresh weight per m^2 of littoral areas, from protected, semi-exposed and fully exposed parts of three districts of the Norwegian coast

District between latitudinal circles	Protected	Semi-exposed	Fully exposed	All
59°30' - 60°30 N	0.81 ± 0.20	0.55 ± 0.13		0.69 ± 0.13
61°30' - 62°N	2.96 ± 0.58	1.46 ± 0.39		2.41 ± 0.40
64° - 67°N	2.11 ± 0.31	0.79 ± 0.11	0.36 ± 0.075	1.44 ± 0.17

When sampling was extended to the whole intertidal zone, the Ascophyllum density was of course lower. It is given for protected and semi-exposed parts of three districts of the Norwegian west coast, in addition to the fully exposed part of one district (Table V). The Ascophyllum density dropped significantly with increasing exposure within the same district. Although sampling errors are high, it also seems highly probable that the overall density of the southern district is lower than that of the two northern ones, probably due to the lesser tidal amplitude of the former. The density difference between the two northern districts (2.41 - 1.44 kg/m^2) is not significant.

Of all ecological factors involved, exposure and sub-stratum are probably responsible for local density differences, whereas tidal amplitudes and temperature may determine regional differences.

4.3 Mortality morbidity

Life span of individuals, see section 4.12.

4.4 Total quantities

Because of its practical importance, estimates have been made of the total quantities of Ascophyllum over large areas.

From a survey covering 4250 miles of Scottish shoreline, Walker (1947) reported 180 713 tons of fresh rockweed, with Ascophyllum as the predominating species. MacFarlane (1952) arrived at 200 000 tons fresh weight in South-West Nova Scotia (325 miles surveyed). From the Murman coast more than 500 000 tons fresh weight have been reported (Zenkevitch, 1963).

The Norwegian Institute of Seaweed Research has tried two methods of rockweed survey, the line survey method and a two-stage, square-scanning sampling method referred to in section 4.2. The two methods gave similar results.

As only selected districts of the Norwegian coast have been surveyed, the total quantity of Ascophyllum available in Norway for commercial use cannot be definitely assessed. However, if the mean values for these districts are extended to neighbouring districts with similar conditions, a total estimate of the order of 1.8 million tons fresh weight is obtained. The actual estimates of error varied between 32 and 39% of the total quantities for the three districts mentioned in Table V. (For details, see Baardseth, 1970b).

It is of course impossible to give a well-founded estimate of the world's total Ascophyllum resources at present, but to judge from the existing estimates and the Ascophyllum areas as yet unsurveyed, it is likely to be of the order of a few million tons fresh weight. For reasons that will be considered later, only a part of this quantity is available for industrial exploitation.

4.5 Accompanying species

A large number of species may be found in the Ascophyllum zone. Only a few of particular interest will be considered here.

Within the territory occupied by Ascophyllum, other fucoids are frequently seen, especially Fucus vesiculosus. The effect of these on the frequency and density of Ascophyllum has been studied by the use of association coefficients (Baardseth, 1955a). It appears that neither the frequency nor the density of Ascophyllum is affected by the presence of F. serratus. If, however, F. vesiculosus or Codium are present, the density of Ascophyllum is significantly reduced. This may be a consequence of composition, but it could also be explained by differences in sub-stratum or exposure.

References are frequently made to the relative position of Ascophyllum and F. vesiculosus on the shore. Although exceptions seem to exist, F. vesiculosus usually grows higher up on the shore than Ascophyllum, and in certain places it is also found below the Ascophyllum zone (as F. vesiculosus f. vadorum).

Walker (1947) gives the ratio of the areas covered by Ascophyllum and F. vesiculosus in Scotland as 100:32, respectively. The weight-ratio is 100:30 in Hitra-Frøya on the Norwegian coast (Baardseth and Grenager, 1961). In a district further north (64°-67°N), the weight-ratio Ascophyllum:F. vesiculosus:F. serratus was found to be 100:39:41.

The following species are among those frequently reported as growing in the Ascophyllum zone:

Plants:
Cladophora rupestris (L.) Kütz.
Chondrus crispus (L.) Stackh.
Gigartina stellata (Stakh.) Batt.
Hildenbrandtia prototypus Nardo
Lithothamnion lenormandii (Aresch.) Fosl.
Ceramium rubrum (Huds.) J.Ag.
Catenella repens (Lightf.) Batt.
(Central Europe)
Rhodocorton purpureum (Lightf.) Rosenv.
(synonymous with R. rothii Naeg.)
Halosaccion ramentaceum (L.) J.Ag.
(Northern distribution)

Animals:
Mytilus edulis
Littorina sp.

Epi-endophytes:
In general, Ascophyllum looks fairly "clean". It is, however, known to be a host for several plants and animals, some of which are confined solely to this species of alga:

- Vertebrata fastigiata (Roth) Gray (synonymous with Polysiphonia fastigiata). This is a common epiphyte in the lower littoral and in exposed localities. In rare and exceptional cases, it has been found on rocks and on Fucus vesiculosus as well.

- Pylaiella litoralis (Lyngb.) Kjellm. According to Kylin (1933) and Levring (1937), the sporophyte of this species sits directly on Ascophyllum, whereas its gametophyte generation grows on Sertularia pumila which, in turn, is attached to Ascophyllum. Pylaiella is a common summer epiphyte on Ascophyllum.

- Ulothrix pseudoflacca Wille. This epiphyte is common in spring, in certain districts.

- Mytilus edulis. This is sometimes seen in damaged vesicles of Ascophyllum, frequently also attached to the holdfast, but is also found on other parts of the plant.

- Sertularia pumila. This is a common zoo-epiphyte.

- Mycosphaerella ascophylli Cotton. Fungal hyphae are never absent from any part of Ascophyllum (Fig. 6, f). They grow in the intercellular spaces, usually in a sterile condition. Whether or not these belong to the species described by Cotton (1908), is unknown to the author. Church (1954) described a fungus in Ascophyllum receptacles with superficial perithecia.

- Navicula endophytica Hasle (1968). The intercellular liquid, squeezed out of the receptacles of Ascophyllum, very frequently contains small diatoms (Fig. 6, d) (Baardseth, 1966). In some instances, between 50 and 100 000 per receptacle were estimated. The diatoms are sometimes also found in growing tips and other parts of Ascophyllum and seem to be associated with the occurrence of water-soluble alginate.

  The distribution of Navicula within an Ascophyllum plant is discontinuous. In samples from the Trondheimsfjord, Norway, 1-4% of the new vesicles were found to be infected in February-April, 19% in June and 35% of older vesicles. In a sample from August 1968, 22% of the linear receptacles had endophytic diatoms, 87% of the spathulate ones and 100% of the globular, gas-inflated ones. In the vegetative parts of Ascophyllum between the vesicles, endophytic diatoms are practically non-existant.

  According to an investigation by Taasen (personal communication), Navicula endophytica is found on both sides of the Atlantic and is only missing in some of the more extreme habitats of its host.

- Cocconeis sp. This diatom is sometimes also found in the receptacles of Ascophyllum.

- Other organisms. Bacteria, Cyanophyceae, diatoms, algae and animals of various kinds other than those mentioned are sometimes seen on Ascophyllum. Their distribution has been little studied.

5. HARVESTING

Harvesting of Ascophyllum for various purposes has been going on for many hundreds of years. It was harvested in the 17th century for the manufacture of soda, but it was probably used at a much earlier time as manure or animal fodder (Chapman, 1950). The Norwegian names "hest-tang" (horse-tang) and "grise-tang" (pig-tang) suggest its early use as fodder.

5.1 Equipment and method of harvesting

No mechanical harvesting equipment has been invented as yet and Ascophyllum is still reaped by hand-cutting. Harvesting and transport are sometimes rationalized by various methods, for instance, by clearing a cart track on the shore. In another method, cut areas are enclosed by a net at low water, the cut weed is allowed to float at high water, and the net is then tied around the algal mass for further transport. The usual way of drying, by spreading the material on rocks, is somewhat risky because rain may spoil it. Hanging is recommended unless the factories receive the material in a fresh condition. In recent years, Norwegian factories have been receiving more than 80% of their total intake in the fresh state.

5.2 Harvesting seasons

Although the commercial harvesting of Ascophyllum seems to be governed by many considerations other than biological ones, it should nevertheless be pointed out that a harvest in late summer probably gives more dry weight per acre and hence a better exploitation of the shore than a harvest at any other time of the year. The properties of the industrial raw material, are considered in sections 7 and 8.

For manure, Ascophyllum is usually harvested by farmers in the spring. For meal production, the summer appears to be the best harvest season, although the modern seaweed industry tends to be based upon year-round production.

5.3 Harvesting areas and depths

Ascophyllum is at present harvested in Canada, the British Isles, France, Iceland and Norway. These are all countries with clearly perceptible tides and the harvest takes place in the intertidal zone, especially in the lower half of it.

5.4 Regrowth on harvested areas

It is a common experience amongst cutters of Ascophyllum that a harvest obtained by scraping the rocks ruins the beds for many years. Fucus vesiculosus occupies the scraped areas at once and Ascophyllum has great difficulty in coming back. The same is seen when a new sub-stratum, for instance a concrete block, is laid down in the intertidal zone. Upon two recently built breakwaters in Norway, F. vesiculosus and F. serratus appeared first, and established themselves as distinct zones, before a few scattered Ascophyllum germlings arrived several years later. An Ascophyllum zone had not established there, even after 8 years. Similar observations were made by Knight and Parke (1950). Breakwaters 30 years old did, however, have such a zone.

If the cutting leaves stumps behind, then these will sprout after some time and lead to regrowth (Fig. 8). A widespread opinion amongst cutters is that it takes 3–6 years before the vegetation is re-established and can be cut again.

In a large-scale experiment (Bjørøyvaer, Norway at 64°N), in which 809 m^2 of the Ascophyllum beds were cut, 4925 kg fresh weight was the initial harvest. After 3 years of undisturbed growth, the area was cut again, giving only 2705 kg or 55% of the original amount. In other experiments, however, 3 years of regrowth were sufficient to restore the original weight of Ascophyllum or even surpass it. The failure to get consistent results from such experiments must be due to different productivty and regenerative powers of the beds themselves and the impossibility of leaving behind the same amount of growing material in every one of the experiments. Generally speaking, however, our experiments showed that it is perfectly possible to restore the original weight after 4–6 years. Some rather pessimistic views about regrowth after commercial harvesting have been expressed (Printz, 1959a and de Virville, 1953), but they are not shared by the present writer. In fact, the regenerative power of well-developed, harvestable beds of Ascophyllum is good, provided the harvesters leave behind a sufficient amount of growing material. This is obviously an important point, but the present writer has been unable to find the exact relation between the amount of the remnant parts and the subsequent regrowth. Stumps 10–20 cm high are frequently recommended although it seems more important to let actively growing shoots remain.

5.5 Total annual yields

Reliable statistics for the annual world harvest of Ascophyllum do not exist (Woodward, 1966). Considering, however, that the annual production of seaweed meal – approximately 50 000 tons (Jensen, Nebb and Saeter, 1968) – is based mainly upon Ascophyllum, and that this species is also harvested for alginate and manure, one will have to assume an annual harvest of a few hundred thousand tons, fresh weight. Chapman (1950) has published a thorough review of the history of the kelp industry with some examples of quantities harvested and prices obtained. Thus 400 000 tons of wet weed were harvested annually in the Hebrides alone

at the beginning of the 19th century. Most of this quantity probably consisted of Ascophyllum.

At present, about 55 000 tons of wet Ascophyllum are harvested in Norway annually for the seaweed meal industry.

It must be emphasized that not all Ascophyllum beds are available for commercial harvest. Some are too far away for economic transport to the factories and some beds are too thin for profitable harvest. Furthermore, large areas with perfectly harvestable Ascophyllum are still without a seaweed industry.

6. PROTECTION AND MANAGEMENT

6.1 Official regulations

In order to promote conservation of the beds, harvesting regulations for Ascophyllum were drawn up by the Department of Lands and Forests of Nova Scotia (MacFarlane, 1964). The present writer is not aware of any other countries having taken official steps to control the harvesting of Ascophyllum.

7. CHEMICAL COMPOSITION

Ascophyllum has been extensively analysed and studied chemically, not only because it serves as raw material for an industry, but also because the plant itself has a considerable basic interest. No attempt will be made here to give a complete review of all recent advances, but the available information about the main or best known constituents, together with their variations with season, locality and age, will be briefly summarized. Additional references are given by Hoppe in Levring-Hoppe-Schmid, 1969. The function of the several organic and inorganic components in the plant is really very little understood and the problem of their localization has barely been touched. The seasonal variation in some constituents is given in Fig. 9 (see also Black, 1948).

7.1 Water content

The water/dry matter content of Ascophyllum has been determined a number of times. The Norwegian seaweed meal industry operates with a conversion factor fresh seaweed/seaweed meal of 3.0 - 3.4. As the finished meal always contains some moisture (Table IX), this conversion factor would correspond to about 25-29% dry matter of the fresh Ascophyllum weight. It is now quite clear that the dry matter content varies with locality and season in addition to the unavoidable individual variation (Baardseth, 1970a; Baardseth and Haug, 1953). During low tide, it also varies with duration of air exposure and weather conditions.

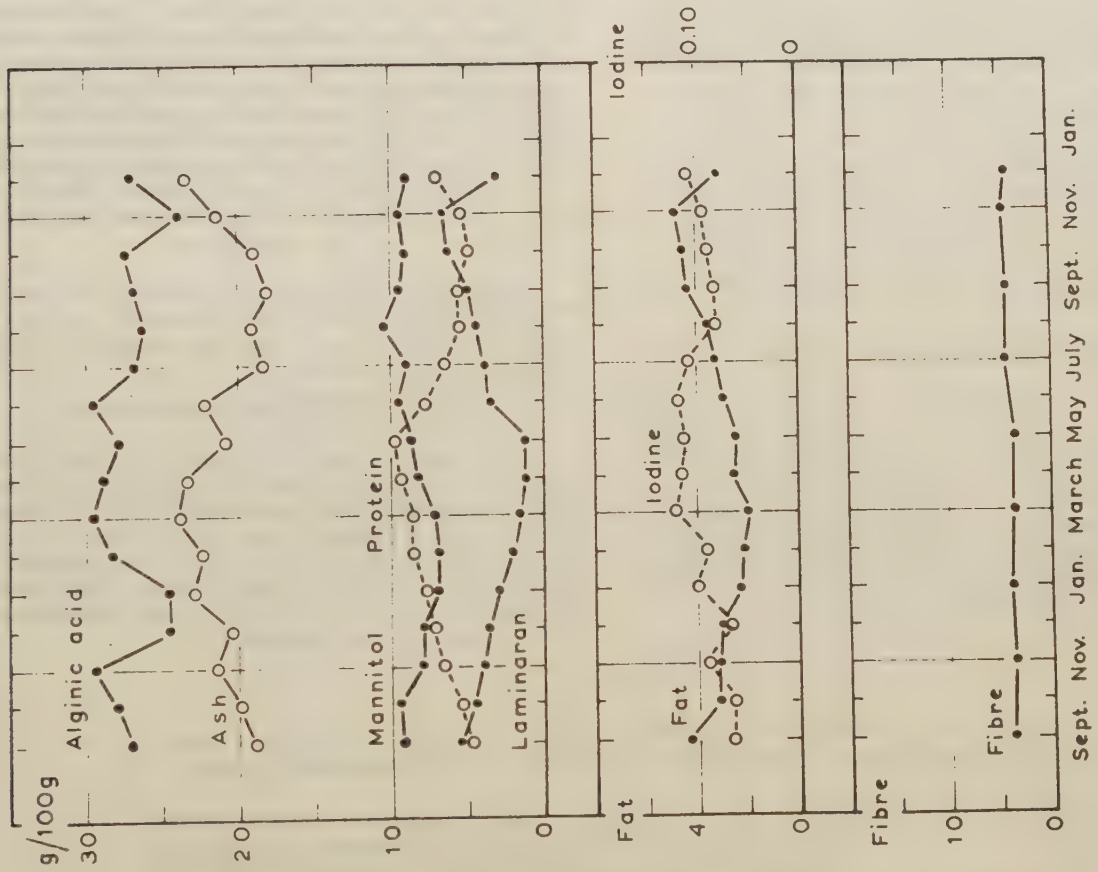


Fig. 9 Seasonal variation in some constituents of Ascophyllum expressed as percentage of dry matter. Samples from Reine, Norway, 1951-52 (Jensen, 1960)

In two series of monthly samples of 10 plants from two contrasting habitats, it was found that 3 seasons could be recognized, a summer, a winter and a ripe fruiting season (Baardseth, 1970a). The percentage of dry matter varied as follows:

Locality	% dry matter		
	Summer season	Winter season	Fruiting season
Leangen	27	23	19
Byneset	29	26	23

The sampling error of all these figures is ± 2%.

Larsen and Haug (1958) found 29.8–31.5% dry matter in open sea localities (summer), dropping down to 24.7% in a locality of low salinity. Munda (1964) transported plants from high to low salinity waters and vice versa. The transported plants adjusted their dry matter content to that of the neighbouring plants within two hours. It thus seems that the dry matter content increases with increasing salinity, and that the plant is able to regulate its water content with salinity changes.

Receptacles isolated from the mother plant had 15–18% dry matter in a low-salinity locality and 19–21% in a high salinity locality during winter. In the ripe period these percentages dropped to 10–11% and 13–14%, respectively, for the two localities (Baardseth, 1970a).

7.2 Inorganic constituents

– Ash content

The mineral content of Ascophyllum as measured by percent ash of dry matter, has been determined a number of times (Vinogradov, 1953). Discrepancies between the results reported by different authors may in part be due to differences in methodology, but there are also seasonal, ecological and individual variations.

In one series of 137 Ascophyllum plants (collected 10 September, from Leangen, Trondheimsfjord), the ash content as determined by heating at 500°C overnight, varied between 18 and 27% of dry matter (Baardseth, 1970a). It therefore appears desirable to take this type of variation into account. The values obtained from this sample were normally distributed. This made it possible to employ the method of analysis of variance to a study of the seasonal variation.

Samples of Ascophyllum collected on the same date showed only small differences from locality to locality, in spite of considerable differences in the salinity of the water (Larsen and Haug, 1958). It seems that plants of the same season maintain a fairly constant relation between salt and organic matter, irrespective of the salinity of the water.

The ratio of salts to organic matter differs, however, from season to season. Table VI gives the mean percentage of ash from vegetative parts, receptacles and whole plant at various seasons and from two contrasting localities. These percentages are based upon a large number of plants. Vegetative parts of the plants consistently show a lower ash content during summer than during the rest of the year. The receptacles have significantly more ash than the vegetative parts and the ash-content rises abruptly during the ripening process. The rise was considerably higher for one locality than for the other, but otherwise the ash content was practically the same for the two localities.

The ash content of two series of seaweed meals (Jensen, 1966a) showed low values in summer and high ones in winter. They are somewhat higher than those mentioned above.

– Major mineral components

The composition of the ash has been determined (see, for example, Vinogradov, 1953), but the published results differ considerably. If Vinogradov's average percentages of the most important ash components are compared with the composition of sea water (Table VII), a marked degree of selectivity is apparent. Obviously, the plant accumulates at least K and SO_4 and rejects Cl.

TABLE VI

Seasonal ash content from vegetative parts, receptacles and whole plant of Ascophyllum. From Leangen and Byneset, Trondheimsfjord, Norway

	% ash of dry matter					
	Summer season		Winter season		Fruiting season	
	Leangen	Byneset	Leangen	Byneset	Leangen	Byneset
Vegetative parts	19.1	19.5	22.4	22.6	22.9	21.3
Receptacles			25.2	25.5	34.5	29.2
Whole plant	19.1	19.5	23.2	23.1	26.8	23.0

TABLE VII

Proportion of major ions in sea water and in ash of Ascophyllum, recalculated from Vinogradov (1953)

Component	% of total salt in sea water	Proportion of ions in ash of Ascophyllum
Na	29.9	19.6
Mg	3.6	5.7
Ca	1.2	7.5
K	1.1	13.3
Cl	53.8	16.8
SO_4	7.5	37.1
Total	97.1	100.0

- Trace elements

In addition to these chief minerals, a considerable number of trace elements has been found. Table VIII gives the content of trace elements and its seasonal variation (Black and Mitchell, 1952). Some of these trace elements have probably passed passively into the plant from the sea water, but the high content of others may indicate selectivity. Also, a large number of other trace elements has been found in Ascophyllum (Vinogradov, 1953).

The mineral content in Ascophyllum meal is given in Table IX, and is taken from Jensen, Nebb and Saeter (1968).

TABLE VIII

Content of trace elements in Ascophyllum.
(From Black and Mitchell, 1952)

Component	mg/kg dry matter in samples		
	Winter	Summer	Spring
Co	0.41	0.73	0.73
Ni	1.5	3.7	4.4
Mo	0.69	0.89	0.29
Fe	168	1150	283
Pb	6	4	4
Sn	1.0	1.1	0.7
Zn	103	116	60
V	1.9	2.8	1.5
Ti	9	28	26
Cr	0.7	1.9	1.0
Ag	0.3	0.1	0.2
Rb	80		
Li	4		
Sr	2600	570	>700
Ba	50	18	13
Mn	50	36	27
Cu	4	12	4

TABLE IX

Average composition of Norwegian seaweed meal
(from Jensen, Nebb and Saeter, 1968)

Component	Content	Component	Content
Moisture	12–15 %	Crude fibre	8 %
Ash	17–20 %	Crude protein	5–10 %
Alginic acid	20–26 %	Ether extract	2– 4 %
Mannitol	5– 8 %	Fucoidan	10 %
Laminaran	2– 5 %	N-free extractives	45–60 %
S	2.5–3.5 %	Caloric value	0.56 SFU/kg*)
K	2– 3 %	Ascorbic acid	500–2000 mg/kg
Cl	3.1–4.4 %	Carotene	30–60 mg/kg
Na	3– 4 %	Biotin	0.1–0.4 mg/kg
Mg	0.5–0.9 %	Folic acid	0.1–0.5 mg/kg
Ca	1– 3 %	Folinic acid	0.1–0.5 mg/kg
P	0.1–0.15 %	Niacin	10–30 mg/kg
B	40–100 mg/kg	Riboflavin	5–10 mg/kg
Co	1–10 mg/kg	Tocopherols	150–300 mg/kg
Fe	150–1000 mg/kg	Vit.B_{12}	0.004 mg/kg
Mn	10–50 mg/kg	Vit.K	10 mg/kg
I	700–1200 mg/kg	V	1.5– 3 mg/kg
Zn	50–200 mg/kg	Ni	2– 5 mg/kg
Mo	0.3– 1 mg/kg	Ba	15–50 mg/kg

*) SFU = Scandinavian feed units

Halogens

The chloride content is given in Tables VII and IX.

The iodine content has been determined a number of times, with results ranging from 0.062 to 0.1984% of the dry matter (Vinogradov, 1953) or from 0.056 to 0.7934% of total ash. In one series (Jensen, 1960) it varied between approximately 0.06 and 0.12 percent of dry matter, the highest value occurring in spring. Similar results were obtained for two series of seaweed meals (Jensen, 1966a).

Bromine is present in approximately the same amounts as iodine (Vinogradov, 1953).

– Nitrate

In one investigation (Larsen and Jensen, (1957), about 0.02–0.04 gN from nitrates was found in 100 g of dry matter from Ascophyllum, without any traceable seasonal variation.

7.3 Organic constituents

The main organic substances of Ascophyllum are fairly well known through numerous analyses in many countries. The most important ones by weight are alginate, mannitol, laminaran, fucoidan, fats, proteins, fibres and phenols. Other organic substances investigated are pigments, vitamins, hormones and enzymes.

7.31 Carbohydrates

The chemical structure and physico-chemical properties of alginates have been extensively studied, and reference is made to monographs by Haug (1964) and Percival and McDowell (1967) for details. Haug includes a detailed account of the composition and properties of alginate from Ascophyllum, together with an evaluation of this species as raw material for the alginate industry. The principal point that must be emphasized here is that alginate from Ascophyllum is not necessarily identical with alginates from other brown algae. The reason for this stems from the discovery

by Fischer and Dörfel (1955) that alginic acid is a binary copolymer, composed of residues of both D-mannuronic (M) and L-guluronic (G) acids. Thus alginates may differ, both in the ratio of these two acids (M/G) and in the way in which they are arranged along the polymer chains (M-, G-sequence). Differences in M-, G-sequence were found to give rise to marked differences in solubility properties (Haug et al., 1967), and differences in the M/G-ratio caused differences in selectivity towards alkaline earth metals (Haug and Smidsrød, 1967). Ascophyllum has played a prominent part in these investigations. Analyses of different types of tissue in Ascophyllum have shown differences in the M/G-ratio, in the M-G-sequence and possibly also in the viccosity and ionic composition of their alginates. One example is given in Haug, Larsen and Baardseth, 1969.

The alginate in the native intercellular substance of the receptacle medulla in Ascophyllum is water-soluble and linked to the cations Na, K, Ca, and Mg. It is remarkable in that it appears to be composed almost entirely of mannuronic acid residues. On the other hand, the alginate of the cell walls of the receptacle medulla is water-insoluble and contains only 64% of mannuronic acid.

Sodium alginate precipitated from solution by certain electrolytes produces at times capillaries in the resulting gel. The appearance of these capillaries varies from unbranched, club-shaped ones when the alginate is taken from young tissue (Baardseth, 1966) to profusely branched fascicles in alginate from old tissue. The reason for these differences is still obscure.

Simultaneously with the division of oogonia and spermatangia into ripe eggs and sperms, there is a gradual change in the intercellular substance of the receptacle. The alginate, which is initially of high viscosity, gradually undergoes degradation, and eventually it disappears completely. At the same time there is an increase in the amount of inorganic salt in the solution (Baardseth, 1969). The mechanism of the degradation of the alginate inside the receptacles is not yet known.

The various methods available for the quantitative determination of the alginic acid content of brown algae are discussed by Haug (1964). The most reliable figure for Ascophyllum appears to be 22-30 g alginic acid per 100 g of dry matter, which is similar to, or perhaps a little more than the figures for Fucus species, but less than those for species of Laminaria. Comparisons between species are a little difficult, however, because of seasonal, individual and age variations. In Ascophyllum, the percentage of alginic acid in the dry matter certainly also differs from tissue to tissue and from part to part, the maximum being located in the receptacles and the minimum in the stipe.

There is no marked seasonal variation in the percentage of alginic acid in Ascophyllum (Haug, 1964), indicating that, once synthesized, alginic acid seems to be a permanent part of the vegetative tissue. However, seasonal changes certainly take place in the alginate from the receptacles, and long-term changes in the alginate part of the vegetative tissue are not out of question.

Alginates are commonly considered as wall substances or at least metabolized wall substances (Hoffman and Andersen, 1955; Kylin, 1915). There can be little doubt, however, that they occur in the intercellular spaces as well (Baardseth, 1966).

Sulphated polysaccharides

Ascophyllum has played a prominent part in the study of the sulphated, acid-soluble carbohydrates of the Phaeophyceae. Originally isolated and described as "fucoidin" (Kylin, 1915), these materials proved to be more complex than was at first believed.

If the whole plant of Ascophyllum is pre-extracted with dilute acid, and then extracted with aqueous sodium carbonate or sodium hydroxide, the extract, after precipitation of alginate by acidification, contains at least four electrophoretically distinct polysaccharides (Larsen, Haug and Painter, 1966a). The slowest moving of these has been described as an acid-soluble form of alginic acid (Myklestad and Haug, 1966). The next slowest is described as ascophyllan (Larsen and Haug, 1963), and is a fairly well-defined substance containing 22.6% fucose, 22.8% xylose, 22.7% sodiumglucuronate, 12.9% half-ester sulphate (i.e. SO_3Na), and 11.8% protein (Larsen, Haug and Painter, 1966b). About 6% of the dry matter of Ascophyllum was estimated to be ascophyllan. The two fast-moving fractions (each representing about 1.5% of the dry weight) contained the same building units as ascophyllan, but differed from it in quantitative composition.

Recent investigations (B. Larsen, personal communication) indicate that different structural parts of the plant may differ in the relative contents of these polysaccharides. Usually, they occur in association with the alginate, but they may also occur isolated from this substance, for instance, in receptacle exudates.

Percival (1967) also isolated a sulphated polysaccharide from Ascophyllum after removal of laminaran, fucoidan and alginic acid. It resembled ascophyllan in containing fucose, xylose, glucuronic acid, sulphate and protein, but differed from it in structure, and the idea of considerable structural variation in material of this type was favoured by the author.

A substance containing fucose, galactose and ester sulphate was isolated from Ascophyllum receptacles by Dillon, Kristensen and O'h Eocha (1953). A liquid squeezed out of the same structures contained, however, also 75–80% of alginate (Baardseth, 1966).

- Laminaran

The study of laminaran has mainly been restricted to the Laminariaceae (Percival and McDowell, 1967). It occurs in Ascophyllum in rather small quantities, 2–5% of the dry matter, with a minimum in spring. It is assumed to be a food reserve, like starch in other plants. Kylin (1915) reports that it occurs as the cold-water soluble form in Ascophyllum. It is not yet clear to what extent the laminaran in Ascophyllum resembles that from the Laminariaceae.

- Mannitol

The quantity of mannitol in Ascophyllum is from 5 to 8 percent in commercial meal (Jensen, Nebb and Saeter, 1968). It is at a minimum during winter and reaches a maximum during summer, although the seasonal variation is not so pronounced as in species of Laminaria. Similar results are reached by Caraës (1969) who also reports on the industrial extraction of this substance from Ascophyllum.

- Other Carbohydrates

Small amounts of glucose (0.1–0.2% of dry matter) are reported by Kylin (1915 and 1944). He considers it to be the first assimilation product, which is then quickly converted into laminaran.

Cellulose is present in small quantities as a wall constituent. Two percent of sellulose has been reported in the dry matter (Percival and McDowell, 1967). In commercial Ascophyllum meal, less than 8% of crude fibres is reported (Jensen, Nebb and Saeter, 1968).

The insoluble residue of Ascophyllum after several extraction procedures was found to be 1.85% of the original dry weight (Young, 1966). It was thought to be composed of cellulose, chitin, and a substance which could be callose.

A large number of component sugars has been found in the total carbohydrate of Ascophyllum: galactose, glucose, mannose, fructose, arabinose, fucose and xylose (Jensen, 1956).

The seasonal variation in L-fucose has been studied by Black (1954).

7.32 Protein and amino acids

The content of crude protein in Ascophyllum meal is 5–10% (Table IX). There does not seem to be any conspicuous or definite variation in protein content with the salinity of the habitat (Larsen and Haug, 1958). A maximum in April–May is evident from Fig. 9.

The amino-acid composition of the total protein has been determined (Coulson, 1953 and 1955; Smith and Young, 1955). Coulson (1955) gives the following figures for amino acid composition of proteins isolated from Ascophyllum (expressed as g of amino acid nitrogen/100 g of protein nitrogen): aspartic acid 8.7, glutamic acid 5.3, serine 3.3, threonine 2.7, glycine 5.7, alanine 5.0, valine + methionine 14.0, leucine + isoleucine 8.7, tyrosine 0.5, arginine 11.8, histidine 0.0, lysine 4.1 (total 59.8). Phenylanaline, proline, tryptophan, and cystine were found but not estimated.

Some amino acids probably occur in the plant in the free state (Larsen and Jensen, 1957).

7.33 Fat

Fat vacuoles are easily demonstrated in the medullary cells of Ascophyllum (Kylin, 1912). The content of ether-extractable substances is 2–4% of dry matter (Jensen, Nebb and Saeter, 1968). Fucosterol was identified by Heilbron (see Lewin, 1962) and a paraffin, probably hentriacontane, was also found in this fraction (Carter, Heilbron and Lythgoe, 1939).

7.34 Pigments

The content and nature of the pigments in Ascophyllum, as well as their variations with season, and changes due to storage and production of seaweed meal are well known, particularly through the recent work of Jensen (1966a), who has also reviewed the literature.

In one series, the content of the four major pigments varied approximately as follows:

	mg/kg dry matter
Chlorophyll a	600–1000
Carotene	40–100
Violaxanthin	60–130
Fucoxanthin	170–270

The carotenoids had a maximum in May, coinciding with and probably caused by the ripening of gametes. According to a later investigation by Jensen (personal communication), the sperms of this period contained enormous quantities of β-carotene (2.4% of dry matter) in contrast to the

eggs with only 0.009%. In addition to β-carotene, the main pigments of ripe eggs were chlorophyll a and c, violaxanthin, fucoxanthin and traces of an unidentified red pigment (see also Carter et al., 1948).

The average content of carotene in commercial seaweed meal (from Ascophyllum) was found to be about 50 mg/kg of dry matter. Meals stored at 4-10°C and with a moisture content of 15% still contained considerable quantities of carotene (15.9-18.8 mg/kg) even after months of storage. However, at higher storage temperatures, the loss in carotene content increased.

Experiments on the storage of fresh material both in air and in sea water have also been done (Jensen, 1966a).

7.35 Other Constituents

- Phenols

The presence of phenols in brown algae has been known for a long time. They are located in a certain type of vacuoles, called physodes, and their presence was readily demonstrated by the colour produced with vanillin-HCl (Crato, 1893). Haug and Larsen (1958) demonstrated that the reducing power of dilute acid extracts from fresh or dried Ascophyllum varied with the salinity of the water. Plants from waters of low salinity yielded extracts with a low reducing power. This fact permitted some correlations to be established. It was found that the reducing power was positively correlated with:

(a) The colour obtained with vanillin-sulphuric acid and with diazotized sulfanilic acid.

(b) The colour intensity of alkaline extracts.

(c) Organic matter which could be removed by hide powder, and which could therefore be classified as "tannins". By this method, approximately 9 g of reducing compounds per 100 g of dry matter was found in the samples with the highest reducing power.

(d) The total volume of the physodes (Baardseth, 1958a). This volume varied between 3 and 10% of the total plant volume (in a fixed condition) according to the salinity of the water.

The amount of phenols in Ascophyllum is therefore quite considerable. Recent observations show, however, that the quantities vary from one part of the plant to another (see section 1.32).

- Vitamins

A large number of vitamins has been studied in Ascophyllum (Ericson, 1953; Jensen, 1964 and 1966a, b; Karlström, 1963; Larsen, 1958 and 1961; Larsen and Haug, 1958). The quantities to be expected in a Norwegian Ascophyllum meal are given in Table IX.

The niacin and biotin contents are at a maximum in spring, and ascorbic acid in summer. There is no loss of niacin during storage of the meal. The ascorbic acid content is gradually reduced, but the loss is dependent upon the moisture content and the storage temperature (Jensen, 1964).

8. UTILIZATION

8.1 Food for human consumption

The eskimos of Western Greenland are reported to use young shoots of Ascophyllum as a dietary supplement (E.A. Saeter, personal communication). There is furthermore evidence that Icelanders have eaten Ascophyllum, but only in times of starvation (Hallsson, 1964). Several attempts have been made to introduce Ascophyllum meal into bread, not because of its calorific value, which is low, but because of its content of vitamins and trace elements (see sections 7.2 and 7.35). So far, these attempts have met with little success, although the tenacity with which Ascophyllum meal remains on the animal-fodder market ought to encourage investigations of its value in the human diet too.

8.2 Animal fodder

There have been numerous reports of sheep and cattle wandering down to the seashore and eating algae voluntarily. This has happened even in periods when grass is plentiful. Ascophyllum does not, however, seem to be their favourite amongst the various species. In one report (from the Orkneys), it is definitely said that sheep do not eat fresh Ascophyllum, in another (from Greenland) that they do (E.A. Saeter, personal communication). There can be no doubt, however, that they prefer such species as Rhodymenia, Laminaria and Alaria.

It is probable that Ascophyllum was given to domestic animals in former times, especially in periods when hay was scarce. It was, however, found necessary to steep it in hot water in order to remove laxative substances before it was given to the animals. The result was a rather inferior type of fodder.

The greater part of all Ascophyllum harvested today is used in the production of seaweed meal. The industry started in Europe at the beginning of this century, but it was not until the late thirties that the industry reached its present degree of stability. From a moderate start, the annual output has gradually increased. In 1958, von Jaken (1958) estimated the annual production to be:

Norway	10 000 tons
France	6–8 000 tons
U.K.	4–5 000 tons
U.S.A.	1–2 000 tons

Norway, France and the United Kingdom employed mainly Ascophyllum as raw material, the U.S.A., Macrocystis. Today, approximately 50 000 tons per year are being produced and in addition to the countries already mentioned, Canada, Ireland, South Africa and Iceland have also started production of seaweed meal (Hallsson, 1964; Jensen, Nebb and Saeter, 1968).

It is quite clear that the success and stability of this industry depend first and foremost upon the real effects produced by the seaweed meal under varying conditions and the confidence that animal breeders have in it. Therefore, the importance of scientific, unprejudiced feeding experiments cannot be overrated. A large number of such experiments has been done recently. A complete review or discussion of all these (see for instance Høie and Sandvik, 1956; Høie and Sannen, 1960; Jensen, Nebb and Saeter, 1968; Nebb and Jensen, 1966), cannot be given here but the main results might be summarized as follows:

(a) Ascophyllum meal must be considered as a supplementary feed and not as an energy source. The content of digestible carbohydrates, fat and protein is low and the meal will not, in this respect, be able to compete economically with other foodstuffs on the market. Five percent of Ascophyllum meal in the total diet is frequently recommended. When an amount of 10% or more is used, the reduction in caloric value is being felt. The laxative effect of seaweed and seaweed meal is frequently referred to. In an actual tolerance experiment, however, Jensen (1958) found no such effect upon sheep even if a ration of 300 g per day per animal was administered. Fifteen percent of Ascophyllum meal in the diet of hens produced a mild laxative effect, but 5-7% had no such effect, either upon chickens or upon laying hens (Høie and Sannan, 1960).

(b) If there is a vitamin deficiency in the ordinary diet, Ascophyllum meal may rectify this (see section 7.35). Of special importance in this type of seaweed meal are β-carotene, tocopherol and some β-vitamins.

(c) Modern agriculture is faced with the problem of replacing minerals and trace elements which are constantly being taken away from the farms with the sale of their products. The use of inorganic salts in both fertilizers and feeding-stuffs is cheap, but complicated, and has sometimes led to disastrous results due to overdosage (Booth, 1964). Ascophyllum meal in ca 5% concentration is at least a harmless source of minerals and trace elements. It is not well balanced, however, as the percentage of some elements (e.g. I and Sr) is above, and that of others (e.g. Ca, P, Mg, Cu) is below the normal requirements. An Ascophyllum meal fortified with Ca, P, Mg and Cu proved superior to the commercial mineral mixtures for milk production in an experiment with twin cows (Jensen, Nebb and Saeter, 1968).

8.3 Manure

The use of Ascophyllum and other seaweed as manure was common in coastal districts in former times. It is still cut for this purpose in Ireland, Scotland, France, England and Iceland. It is either put directly on the soil or is first allowed to decompose in heaps. Recently, a liquid fertilizer made by digesting Ascophyllum with hot aqueous sodium carbonate under pressure has been put on the market (Booth, 1966; Milton, 1964).

A large number of experiments have been carried out in order to determine the manurial value of seaweeds. The literature is reviewed by Chapman (1950) and Booth (1964, 1966). Descriptions of actual experiments are given by Challen and Hemingway (1966), Stephenson (1966), and Myklestad (1964). The results are somewhat controversial, but on the whole there seems to be agreement that seaweeds may be valuable as a source of trace elements and may function as a soil conditioner. It is not unreasonable to expect a soil conditioning effect, in view of the high ion-exchange capacity of the alginate and sulphated polysaccharides. Moreover, oxidation of the phenols present in seaweed can be expected to yield acidic polymers related to the humic acids. A reported effect of seaweed extracts on fungal diseases and insect pests is interesting (Stephenson, 1966). Also, increase in seed germination and increase in the uptake of nutrients are reported by use of seaweed manure (Booth, 1966).

8.4 Industrial products

Ascophyllum was once considered to be inferior as a raw material for the production of alginate because the final product tended to be discoloured and of low viscosity. These disadvantages are due to the presence of phenolic compounds (Haug, 1964) which are responsible for oxidative degradation of the alginate during the extraction process and for the simultaneous formation of brown polymeric material. This is now avoided by pretreatment of the raw material with formalin and by the careful control of pH during extraction. With these precautions, Ascophyllum is not an inferior raw material although most factories still seem to prefer Laminaria digitata if there is the possibility of choice between these two algae. Both an English and a Canadian firm utilize Ascophyllum in their alginate production.

Commercial alginates differ in their content of impurities, in viscosity, uronic acid composition, selectivity towards ions etc. (Haug. 1964). This is partly due to the use of a variety of species as raw material. Because alginates serve very different purposes in the industry, one may foresee a development towards greater care in choosing the right type of alginate for the purpose in question. It may well be that for certain purposes alginate from certain species of algae are required and that Ascophyllum alginate will be more suitable in some cases.

9 REFERENCES

Alstadsaeter, I., 1954 Algological observations in the Hardanger Fjord. Nytt Mag.Bot., 2:101-16

Baardseth, E., 1955a A statistical study of the structure of the Ascophyllum zone. Rep.Norw.Inst.Seaweed Res., (11):34 p.

_____, 1955b Regrowth of Ascophyllum nodosum after harvesting. Dublin, Institute for Industrial Research and Standards, 63 p.

_____, 1958a A method of estimating the physode content in brown algae. Rep.Norw.Inst.Seaweed Res., (20):1-6

_____, 1958b The quantitative composition of the fucoid zone. Rep.Norw.Inst.Seaweed Res., (20):7-10

_____, 1966 Localization and structure of alginate gels. Proc.int.Seaweed Symp., 5:19-28

_____, 1969 Some aspects of the native intercellular substance in Fucaceae. Proc.int.Seaweed Symp., 6:53-60

_____, 1970a Seasonal variation in Ascophyllum nodosum (L.) Le Jol. in the Trondheimsfjord with respect to the absolute live and dry weight and the relative contents of dry matter, ash and fruit bodies. Botanica mar., 7(1):1-11

_____, 1970b A square-scanning, two-stage sampling method of estimating seaweed quantities. Rep.Norw. Inst.Seaweed Res., (33):41 p.

Baardseth, E. and A. Haug, 1953 Individual variation of some constituents in brown algae, and reliability of analytical results. Rep.Norw.Inst.Seaweed Res., (2):23 p.

Baardseth, E. and B. Grenager, 1961 A method of estimating seaweed quantities. Rep.Norw.Inst.Seaweed Res., (25):39 p.

Bergquist, P.L., 1959 A statistical approach to the ecology of Hormosira banksii. Botanica mar., 1(1-2): 22-53

Black, W.A.P., 1948 Seasonal variation in chemical composition of some of the littoral seaweeds common to Scotland. Part 1. Ascophyllum nodosum. J.Soc.chem.Ind., London, 67:355-7

_____, 1954 The seasonal variation in the combined L-fucose content of the common British Laminariaceae and Fucaceae. J.Sci.Fd Agric., 5:445-8

Black, W.A.P. and R.L. Mitchell, 1952 Trace elements in the common brown algae and in sea water. J.mar.biol. Ass.U.K., 30:575-85

Boney, A.D., 1968 Experiments with some detergents and certain intertidal algae. The biological effects of oil pollution on littoral communities. Fld Stud., 2, Suppl.

Booth, E., 1964 Trace elements and seaweeds. Proc.int.Seaweed Symp., 4:385-92

_____, 1966 Some properties of seaweed manures. Proc.int.Seaweed Symp., 5:349-57

Caraës, A., 1969 Le Mannitol dans les Phéophycées et son extraction industrielle. Proc.int.Seaweed Symp., 6:663-9

Carter, P.W., J.M. Heilbron and B. Lythgoe, 1939 The lipochromes and sterols of the algal classes. Proc.R. Soc., 128:82-109

Carter, P.W. et al., 1948 The lipochromes of the male and female gamets of some species of the Fucaceae. Biochem.J., 43:349-52

Challen, S.B. and J.C. Hemingway, Growth of higher plants in response to feeding with seaweed extracts.
1966 Proc.int.Seaweed Symp., 5:359-65

Chapman, V.J., Seaweed and their uses. London, Methuen & Co. Ltd., 287 p.
1950

Church, A.H., A marine fungus. Ann.Bot., 7:399-400
1954

Cotton, A.D., Notes on marine Pyrenomycetes. Trans.Br.mycol.Soc., 3:92-9
1908

Coulson, C.B., Protein of marine algae. Chem.Inds,Lond., 1953:997-8
1953

_____, Plant proteins. 5. Proteins and amino acids of marine algae. J.Sci.Fd Agric., 6:674-82
1955

Crato, E., Morphologische und mikrochemische Untersuchungen über die Physoden. Bot.Ztg., 51:157-95
1893

Crisp, D.J. and E. Fischer-Piette, Répartition des principales espèces intercotidales de la côte
1959 Atlantique française. Annls Inst.océanogr.,Monaco, 36(2):275-388

David, H.M., Studies in the autecology of Ascophyllum nodosum Le Jol. J.Ecol., 31:178-98
1943

Davidson, F.F., The effect of auxin on the growth of marine algae. Am.J.Bot., 37:501-10
1950

Davy de Virville, A., Dépeuplement de la flore marine sur les côtes occidentales du Cotentin. Proc.
1953 int.Seaweed Symp., 1:26-8

De Toni, J.B., Sylloge algarum omnium hucusque cognitarum. Fucoideae. Padova, Tip.del Seminario,
1895 vol. 3

Dillon, T., K. Kristensen and C. O'h Eocha, The seed mucilage of Ascophyllum nodosum. Proc.R.Ir.Acad.,
1953 55:189-94

Doty, S. and J. Newhouse, The distribution of marine algae into estuarine waters. Am.J.Bot., 41:508-15
1954

Ericson, L.E., On the vitamin B_{12}-, folic acid-, and folinic acid groups of factors and on the occurence
1953 of these vitamins and of niacin, pantothenic acid and amino acids in a number of marine algae.
Stockholm, Tekniska Högskolan (MS)

Feldmann, J. and R. Lami, Flore et végétation marines de la côte basque française. Bull.Soc.bot.Fr.,
1941 88:123-42

Fischer, F.G. and H. Dörfel, Die Polyuronsäuren der Braunalgen. Hoppe-Seyler's Z.physiol.Chem., 302:
1955 186-203

Fischer-Piette, E. and J. Seoane-Camba, Ecologie de la ria-type: la Ria del Barquero. Bull.Inst.
1962 océanogr.,Monaco, 59(1244):36 p.

_____, Examen écologique de la Rina de Camariñas. Bull.Inst.océanogr.,Monaco, 61(1277):38 p.
1963

Fritsch, F.E., The structure and reproduction of the algae. Cambridge, University Press, vol. 2:939 p.
1945

Gibb, D.C., The free-living forms of Ascophyllum nodosum (L.) Le Jol. J.Ecol., 45:49-83
1957

Gislén, T., Epibioses of the Gullmar Fjord. 2. Marine sociology (Kristinebergs Zoologiska Station, 1930 1877-1927). Skr.Ser.K.svenska Vetensk Akad., (4):1-380

Godward, M.B.E. (ed.), The chromosomes of the algae. London, Edward Arnold (Publishers) Ltd., 222 p. 1966

Grenager, B., Algological observations from the polluted area of the Oslofjord. Nytt Mag.Bot., 5:41-60 1937

Grenager, B. and E. Baardseth, A two-stage sampling method of estimating seaweed quantities. Proc.int. 1966 Seaweed Symp., 5:129-35

Hallsson, S.V., The uses of seaweeds in Iceland. Proc.int.Seaweed Symp., 4:398-405 1964

Harvey, W.H., Phycologia Britannica: A history of British seaweeds. Melanospermeae, or olive seaweeds. 1871 Synopsis, No. 1 to 97. London, L. Reeve & Co., vol. 1 :192 p.

Hasle, G.R., Navicula endophytica, sp. nov., a pennate diatom with an unusual mode of existence. 1968 Br.phycol.Bull., 3(3):475-80

Haug, A., Composition and properties of alginate. Rep.Norw.Inst.Seaweed Res., (30):123 p. 1964

Haug. A. and B. Larsen, Phenolic compounds in brown alga. Acta chem.scand., 12:650-57 1958

Haug, A. and O. Smidsrød, Strontium - calcium selectivity of alginates. Nature,Lond., 215:757 1967

Haug, A., B. Larsen and E. Baardseth, Comparison of the constitution of alginates from different 1969 sources. Proc.int.Seaweed Symp., 6:443-51

Haug, A. et al., Correlation between chemical structure and physical properties of alginate. Acta chem. 1967 scand., 21:768-78

Hoffmann, C. and G. Andersen, Polarisationsoptische Untersuchungen an Laminaria und Fucus. Kieler 1955 Meeresforsch., 11:149-59

Høie, J. and Ø. Sandvik, Experiments with seaweed meals as supplements to rations for chicks and 1956 laying hens. Proc.int.Seaweed Symp., 2:82-97

Høie, J. and F. Sannan, Experiments with seaweed meals as supplements to rations for chicks and 1960 laying hens. 2. Meld.Norg.LandbrHøisk., (39):76 p.

Jensen, A., Component sugars of some common brown algae. Rep.Norw.Inst.Seaweed Res., (9):8 p. 1956

_____, Experiments on the feeding of seaweed meal to domestic animals. Rep.Norw.Inst.Seaweed 1958 Res., (20):25-28

_____, Produksjon av tangmel. Rep.Norw.Inst.Seaweed Res., (24):23 p. 1960

_____, Ascorbic acid in Ascophyllum nodosum, Fucus serratus and Fucus vesiculosus. Proc.int. 1964 Seaweed Symp., 4:319-25

_____, Carotenoids of Norwegian brown seaweeds and of seaweed meals. Rep.Norw.Inst.Seaweed Res., 1966a (31):139 p.

_____, Tocopherol determination in seaweeds. Proc.int.Seaweed Symp., 5:281-6 1966b

Jensen, A., H. Nebb and E.A. Saeter, The value of Norwegian seaweed meal as a mineral supplement for
1968 diary cows. Rep.Norw.Inst.Seaweed Res., (32):35 p.

Jónsson, H., The marine algae of East Greenland. Meddr Grønland, 30
1904

Jorde, I. and N. Klavestad, The natural history of the Hardangerfjord. 4. The benthonic algal
1963 vegetation. Sarsia, (9):99 p.

Karlström, O., The vitamin B_{12} content of marine algae. Rep.Norw.Inst.Seaweed Res., (29):10 p.
1963

Kjellman, F.R., Norra Ishafvets algflora. In Vegaexpeditionens vetenskapliga iakttagelser, vol. 3
1883

Knight, M. and M. Parke, Biological study of Fucus vesiculosus L. and F. serratus L. J.mar.biol.Ass.
1950 U.K., 29(2):439-514

Kylin, H., Über die Inhaltskörper der Fucoideen. Ark.Bot., 11(5)
1912

_____, Untersuchungen über die Biochemie der Meeresalgen. Hoppe-Seyler's Z.physiol.chem., 94
1915

_____, Über die Entwicklungsgeschichte der Phaeophyceen. Acta Univ.lund.(2), 29(7)
1933

_____, Über die Biochemie der Phaeophyceen. Acta Univ.lund., 4(18):1-13
1944

Larsen, B., The influence of season, habitat and age of tissue on the niacin content of some brown
1958 algae. Rep.Norw.Inst.Seaweed Res., (19):13 p.

_____, The biotin content of marine algae. Rep.Norw.Inst.Seaweed Res., (26):18 p.
1961

Larsen B. and A. Haug, The influence of habitat on the chemical composition of Ascophyllum nodosum (L.)
1958 Le Jol. Rep.Norw.Inst.Seaweed Res., (20):29-38

_____, Polysaccharides occurring in the sodium carbonate extracts of Ascophyllum nodosum.
1963 Proc.int.Seaweed Symp., 4:338-43

Larsen, B., A. Haug and T.J. Painter, Sulphated polysaccharides in brown algae. 1. Isolation and
1966a preliminary characterisation of three sulphated polysaccharides from Ascophyllum nodosum (L.) Le Jol. Acta chem.scand., 20:219-30

_____, Preparation and structural investigation of ascophyllan. Proc.int.Seaweed Symp.,
1966b 5:287-94

Larsen, B. and A. Jensen, The determination of nitrate and nitrite in algal material, and the
1957 seasonal variation in the nitrate content of some Norwegian seaweeds. Rep.Norw.Inst. Seaweed Res., (15):22

Le Jolis, A., Liste des algues marines de Cherbourg. Mem.Soc.sci.nat.Cherb., 10:168 p.
1863

Levring, T., Untersuchungen aus dem Öresund 19. Zur Kenntnis der Algenflora von Kullen und der
1935 schwedischen Westküste. Acta Univ.lund.(2), 31(4):1-63

_____, Zur Kenntnis der Algenflora der norwegischen Westküste. Acta Univ.lund.(2), 33(8)
1937

_____, Submarine daylight and the photosynthesis of marine algae. Göteborgs K.Vetensk.-o.
1947 VitterSamh.Handl.(B), 5(6):89 p.

Levring, T., H.A. Hoppe and O.J. Schmid, Marine Algae - A survey of research and utilization. 1969 Botanica mar.Handbk, (1):421 p.

Lewin, R.A. (ed.), Physiology and biochemistry of algae. New York, Academic Press, 929 p. 1962

Lewis, J.R., The ecology of rocky shores. London, English Universities Press, 323 p. 1964

Linnaeus, C., Species plantarum. Holmiae. p. 1159 1753

MacFarlane, C., Observations on the annual growth of Ascophyllum nodosum. Proc.Trans.Nova Scotian 1932 Inst.Sci., 1932:27-33

_____, A survey of certain seaweeds of commercial importance in Nova Scotia. Can.J.Bot., 1952 30:78-97

_____, The seaweed industry of the maritime provinces. Proc.int.Seaweed Symp., 4:414-19 1964

Milton, R.F., Liquid seaweed as a fertilizer. Proc.int.Seaweed Symp., 4:428-31 1964

Munda, I., The influence of salinity on the chemical composition, growth and fructification of some 1964 Fucaceae. Proc.int.Seaweed Symp., 4:123-6

Myklestad, S., Experiments with seaweed as supplemental fertilizer. Proc.int.Seaweed Symp., 4:432-8 1964

Myklestad, S. and A. Haug, Studies on the solubility of alginic acid from Ascophyllum nodosum at low 1966 pH. Proc.int.Seaweed Symp., 5:297-303

Nath, H., Der Einfluss verschiedener Sauerstoffspannungen und salzgehalte auf die Sauerstoffaufnahme 1967 mariner Braun und Grünalgen. Botanica mar., 10(3/4):198-239

Nebb, H. and A. Jensen, Seaweed meal as source of minerals and vitamins in rations for dairy cows and 1966 bacon pigs. Proc.int.Seaweed Symp., 4:387-93

Oltmanns, F., Beiträge zur Kenntnis der Fucaceen. Biblthca bot., 14:1-94 1889

Papenfuss, G.F., Review of the genera of algae described by Stackhouse. Hydrobiologia, 2(3):181-208 1950

Percival, E. Glucuronoxylofucan, a cell wall polysaccharide of the Phaeophyceae. Chem.Inds,Lond., 1967 (12):511

Percival, E. and R.H. McDowell, Chemistry and enzymology of marine algal polysaccharides. London, 1967 Academic Press, 219 p.

Printz, H., Die Algenvegetation des Trondheimsfjordes. Skr.norske VidenskAkad., (5):273 p. 1926

_____, Seasonal growth and production of dry matter in Ascophyllum nodosum (L.) Le Jol. 1950 Avh.norske VidenskAkad.Oslo, (4):15 p.

_____, Norges forekomster av drivtang og drivtare. Rep.Norw.Inst.Seaweed Res., (18):50 p. 1957

_____, Investigations of the failure of recuperation and repopulation in cropped Ascophyllum 1959a nodosum. Skr.norske VidenskAkad., (3):15 p.

Printz, H., 1959b Phenelogical studies of marine algae along the Norwegian coast. Avh.norske VidenskAkad., (4):28 p.

Reinke, J., 1889 Algenflora der Westlichen Ostsee, deutschen Antheils:eine systematisch-pflanzengeographische Studie. Ber.Kommn wiss.Unters.dt.Meere, 6

Rosenvinge, L.K., 1926 Marine algae collected by dr. H.C. Simmons during the 2nd Norwegian Arctic expedition in 1898-1902. Rep.Norw.Arct.Exped.Fram, 2(37):40 p.

Schmidt, O.C., 1931 Die marine Vegetation der Azoren in ihren Grundzügen dargestellt. Biblthca bot., 25(102): 1-116

Setchell, W.A., 1920 Stenothermy and zone-invation. Am.Natst, 54:385-97

_____, 1922 Cape Cod in its relation to the marine flora of New England. Rhodora, 24(277):1-11

Smith, D.C. and E.G. Young, 1955 The combined amino acids in several species of marine algae. J.biol.Chem., 217:845-53

Stephenson, W.M., 1966 The effect of hydrolysed seaweed on certain plant pests and diseases. Proc.int. Seaweed Symp., 5:405-15

Sundene, O., 1953 The algal vegetation of Oslofjord. Skr.norske VidenskAkad., (2):244 p.

_____, MS Growth and reproduction in Ascophyllum nodosum (L.) Le Jol.

Svendsen, P., 1959 The algal vegetation of Spitsbergen. A survey of the marine flora of the outer part of Isfjorden. Skr.norsk Polarinst., (116):1-47

Taylor, Wm.R., 1957 Marine algae of the northeastern coast of North America. Univ.Mich.Stud.scient.Ser., (13):509 p.

Vinogradov, A.P., 1953 The elementary chemical composition of marine organisms. Mem.Sears Fdn Mar.Res., (2):647 p.

von Haken, W., 1958 Algenchemie - ein neuer Wirtschaftszweig. Chem.Ind.Düsseld., 10:246-50

Walker, F.T., 1947 A seaweed survey of Scotland - Fucaceae. Proc.Linn.Soc.Lond., 159(2):90-9

Wilce, R.T., 1959 The marine algae of the Labrador Peninsula and northwest Newfoundland (ecology and distribution). Bull.natn.Mus.Can., (158):105 p.

Woodward, F.N., 1966 The seaweed industry of the future. Proc.int.Seaweed Symp., 5:55-69

Young, E.G., 1966 The chemical nature of the insoluble residue after severe extraction in some Rhodophyceae and Phaeophyceae. Proc.int.Seaweed Symp., 5:337-46

Zenkevitch, L., 1963 (Trans.S.Botcharskaia), Biology of the seas of the U.S.S.R. London, George Allen & Unwin Ltd., 955 p.

SYNOPSIS OF FISHERIES BIOLOGICAL DATA

This is one of a series of documents issued by FAO, CSIRO and USFWS concerning species and stocks of aquatic organisms of present or potential economic interest. The primary purpose of this series is to make existing information readily available to fishery scientists according to a standard pattern, and by so doing also to draw attention to gaps in knowledge. It is hoped that synopses in this series will be useful to other scientists initiating investigations of the species concerned or of related ones, as a means of exchange of knowledge among those already working on the species, and as the basis for comparative study of fisheries resources. They will be brought up to date from time to time as further information becomes available either as revisions of the entire document or their specific chapters.

The relevant series of documents are:

FAO	**Fisheries Synopsis No.** replacing, as from 1.1.63 FAO Fisheries Biology Synopsis No.	FIR/S FB/S
CSIRO	**Fisheries Synopsis No.**	DFO/S
	and	
USFWS FAO	**Fisheries Synopsis No.**	BCF/S

Synopses in these series are compiled according to a standard outline described in FIb/S1 Rev. 1 (1965).

FAO, CSIRO and USFWS are working to secure the cooperation of other organizations and of individual scientists in drafting synopses on species about which they have knowledge, and welcome offers of help in this task. Additions and corrections to synopses already issued will also be most welcome. Comments including suggestions for the expansion of the outline and requests for information should be addressed to the coordinators and editors of the issuing organizations.

FAO:
Fishery Resources Division
Marine Biology and Environment Branch
Food and Agriculture Organization
of the United Nations
Via delle Terme di Caracalla
00100 Rome, Italy

USFWS:
Department of the Interior
Bureau of Commercial Fisheries
Office of Scientific Publications
Building 67, US Naval Air Station
Seattle, Washington 98115, USA.

CSIRO:
Scientific Editor
CSIRO Division of Fisheries and Oceanography
Box 21
Cronulla, N.S.W.
2230 Australia

Consolidated lists of species or groups covered by synopses issued to date or in preparation will be issued from time to time. Requests for copies of synopses should be addressed to the issuing organization.

The following synopses in this series have been issued since January 1969:

BCF/S40	Synopsis of biological data on the Pacific mackerel *Scomber japonicus* Houttuyn (Northeast Pacific)	February 1969
FRi/S30 Rev. 1	Synopsis of biological data on the pike *Esox lucius* (Linnaeus) 1758	May 1969
DFO/S3	Synopsis of biological data on the tiger prawn *Penaeus esculentus* Haswell, 1879	July 1969
FRm/S43	Synopsis of biological data on the anchoveta *Cetengraulis mysticetus* Günther, 1866	October 1969
FRh/S35 Rev. 1	Synopsis of biological data on West African croakers *Pseudotolithus typus, P. senegalensis* and *P. elongatus*	November 1969
BCF/S42	Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*	November 1969
FRm/S78	Synopsis of biological data on smelt *Osmerus eperlanus* (Linnaeus) 1758	December 1969
FIRI/S80	Synopsis of biological data on the eel *Anguilla anguilla* (Linnaeus) 1758 (Provisional version)	April 1970
DFO/S4	Synopsis of biological data on the rainbow prawn, *Parapenaeopsis sculptilis* (Heller, 1862)	1970
BCF/S4	Synopsis of biological data on chum salmon *Oncorhynchus keta*	July 1970
DFO/S5	Synopsis of biological data on the school prawn *Metapenaeus macleay* (Haswell, 1879)	1970
FIRI/S80 Rev. 1	Synopsis of biological data on the eel *Anguilla anguilla* (Linnaeus) 1758	October 1970
FIRM/S82	Synopsis of biological data on North Atlantic sand eels of the genus *Ammodytes (A. tobianus, A. dubius, A. americanus* and *A. marinus)*	November 1970
FIRM/S83	Synopsis of biological data on *Saccorhiza polyschides*	November 1970
FIRM/S38 Rev. 1	Synopsis of biological data on knobbed wrack *Ascophyllum nodosum* (Linnaeus) Le Jolis	December 1970

MI/B0672/1.71/E/1/750